

Durham E-Theses

Sexual differences in behaviour and morphology of Northern Gannets

Redman, Kelly Kristina

How to cite:

Redman, Kelly Kristina (2001) *Sexual differences in behaviour and morphology of Northern Gannets*, Durham theses, Durham University. Available at Durham E-Theses Online: <http://etheses.dur.ac.uk/3803/>

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

Sexual Differences in Behaviour and Morphology of Northern Gannets

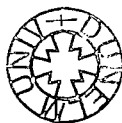
The copyright of this thesis rests with the author. No quotation from it should be published in any form, including Electronic and the Internet, without the author's prior written consent. All information derived from this thesis must be acknowledged appropriately.

Kelly Kristina Redman

Presented in candidature for the degree of

Master of Science

Department of Biological Sciences
University of Durham, U. K.
2001



26 APR 2002

Sexual Differences in Behaviour and Morphology of Northern Gannets

M.Sc. thesis submitted by Kelly Kristina Redman, 2001

ABSTRACT

Northern Gannets (*Morus bassanus*) are large, long-lived seabirds with negligible sexual size dimorphism. In common with other species where the sexes appear similar, very little is known about the differences in breeding behaviour of males and females. I used DNA-based sexing to investigate the accuracy of externally measured biometrics, plus morphological and behavioural observations for sexing breeding birds. I then measured how foraging trip durations, nest attendance patterns and levels of non-attendance by males and females changed during chick-rearing.

All individuals were sexed correctly from nape biting behaviour, but other variables were less successful as a result of lower accuracy and/or because they could be recorded only relatively infrequently. Males spent a significantly higher proportion of time at the nest than females (53% and 42% respectively) and made shorter, more frequent foraging trips than females (mean = 17.3 hours S.D. \pm 8.2, and mean = 21.0 hours S.D. \pm 8.4 respectively). The frequency of food delivery by males increased with increasing chick age, but food delivery rates by females did not change as chicks grew. These data may indicate a greater contribution to food provisioning by males than females. The proportion of time that chicks were left unattended increased with chick age, while males were more likely to leave chicks unattended than females. This probably resulted from males making a trade-off between protecting the chick and providing food for the chick or foraging for themselves. The degree of equitability in foraging trips and nest attendance were not related to either chick hatching date or fledging success.

CANDIDATE'S DECLARATION

I declare that no part of this work has been submitted for any other degree. All the work presented within is entirely my own, unless otherwise stated.

K. K. Redman

2001

© The copyright of this thesis rests with the author. No quotation from it should be published without their prior written consent and information derived from it should be acknowledged.

ACKNOWLEDGEMENTS

Three years ago I decided to look into Masters degrees in England. The first person I spoke with at Durham was Prof. Peter Evans, and he went out of his way to capture my interest and make me seriously consider a post-graduate degree in the U.K. I am grateful to him for his enthusiasm, and interest in me as a student, because I know that without him I would not have begun, let alone finished my Masters thesis in this lovely city. Since my arrival, I have received support from countless people here in Durham and elsewhere. Dr. Keith Hamer has given me volumes of encouragement and support. He's spent countless hours pouring over draft after draft of this thesis, challenging me to improve my skills and take as much away from this experience as I can, and I am grateful to him for that.

There are several people who helped me when I was in Ireland during fieldwork. Martin and Lynda Smyth were friends in Kilmore Quay who opened their home to me in times of need, filling my stomach with fabulous food and giving me a "home base" when times were rough. I will never forget their generosity. I am grateful to Alyn Walsh for his generosity and for sharing his experience with me and teaching me how to take blood samples from those pesky gannets. Oscar Merne was a fountain of knowledge about the island and I thank him for his help with the logistics involved with my working there. He and his wife, Margaret, were also kind enough to open their home to me, as were Ann and David Lewis, in Wales. Thank you both for the late night lifts from the ferry station and your hospitality. Declan and William Bates were experts at riding the waves to get us on and off the island no matter how high the swells were. I am thankful to the Neale family for allowing me access to such a lovely island, how fortunate they are! I would also like to thank Dr. Richard Griffiths, Dr. Francis Daunt, Kate Orr, and Aileen Adam for performing the DNA analysis on the blood of the birds in this study.

There are several people in California who have encouraged and supported me through this degree. First and foremost, my family have been supportive, in

many ways, of me studying so far away from home. I feel lucky because I know they would love to have me at home with them, but they understand where my heart is and support my decision to be here. Dr. Catherine Toft and Jennifer Housley have both encouraged me to follow my ecological aspirations, and Dr. Jon Eadie first taught me the wonders of birds, and to them I am grateful.

I am lucky to have the friendship of those I met when I was at Lancaster University, especially Steven Porter who was my pillar of strength for many years, and a strong influence on my feelings for England, and a continual support (technical and otherwise) throughout my stay in Durham.

And then there was Durham - It's lovely. Through the past year I have called on several people here at Durham to lend support. Eric Henderson and Michael Bone were very helpful with pre-season preparations and made sure Sue and I were safe and well equipped on Saltee. Jonathon Bennie was a fabulous rock-climbing partner, and a good friend who helped me immensely by reading several drafts of chapters in progress. Catherine Gray, Kathy Fletcher, and Sue Lewis were invaluable with their advice, chapter revisions, and general support, as were Robin Ward, Dr. Jane Hill, Matthew Davey, Ruth Cox and Ann Harding. Andrew Hardisty saved the day on many occasions with his computer expertise. A big thank you to Catherine Gray, Sue Lewis, Dimitris Giantzoudis, and Sean Twiss for giving me somewhere to stay in Durham when I was in need of a bed. Thank you to Dr. Richard Phillips who sent papers, and brainstormed ideas with me for my sexing chapter. I am thankful to Newby Trust Limited and the Graduate Society Hardship Fund, Durham University for help with funding.

Finally, I would like to send a big thank you to Sue Lewis for making our experience on Great Saltee Island as pleasant as possible. We worked hard, we laughed hard, and what more could we have asked for?

TABLE OF CONTENTS

<i>Abstract</i>	<i>i</i>
<i>Declaration</i>	<i>ii</i>
<i>Acknowledgements</i>	<i>iii</i>
<i>Table of Contents</i>	<i>v</i>
<i>List of Figures</i>	<i>vii</i>
<i>List of Tables</i>	<i>viii</i>
Chapter 1 General Introduction	1
1.1 Seabird Life Histories	5
1.2 Northern Gannets	8
1.3 The Study Site	10
1.4 Aims and Objectives	11
Chapter 2 Sexing Gannets by DNA, Behaviour and Morphology.....	14
2.1 Introduction	15
2.2 Methods.....	17
2.3 Results	21
2.3.1 Biometrics	21
2.3.2 Morphology and Behaviour	22
2.3.3 Seasonal Variation	23
2.4 Discussion	24

Chapter 3 Foraging and Nest Attendance Patterns of Males and Females.....	30
3.1 Introduction.....	31
3.2 Methods.....	34
3.3 Results.....	36
3.3.1 Nest Attendance	36
3.3.2 Trip Durations	37
3.3.3 Non-attendance	38
3.3.4 Equitability in foraging and nest attendance of males and females	39
3.4 Discussion	46
3.4.1 Nest Attendance	46
3.4.2 Trip Durations	47
3.4.3 Non-Attendance	49
3.4.4 Equitability in foraging and nest attendance of males and females	49
 Chapter 4 General Discussion.....	 51
 References	 57

LIST OF FIGURES

Figure 1-1: Location of Great Saltee Island, Ireland.	12
Figure 1-2: Map of Great Saltee Island, Ireland with notation of the two gannet colonies.	13
Figure 3-1: Proportion of time (± 1 S.E.) spent at the nest by males (closed circles) and females (open circles) in relation to chick age.	41
Figure 3-2: Proportion of time (± 1 S.E.) spent by parents together at the nest site in relation to chick age.	42
Figure 3-3: Frequency distribution of average foraging trip durations at each nest, for male (black) and female (white) gannets.	43
Figure 3-4: Foraging trip durations (± 1 S.E.) of male (solid circles) and female (open circles) gannets in relation to chick age.	44
Figure 3-5: Proportion of the total observation period (± 1 S.E.) when chicks were left unattended.	45
Plate 2-1: Example of the chart used in observations to obtain consistency in head and web-line colour assessment.	20

LIST OF TABLES

Table 2-1: Morphometric data for gannets on Great Saltee Island.	21
Table 2-2: Effectiveness of four techniques for sexing gannets.	22
Table 2-3: The ability of different techniques to sex gannets at different stages of chick-rearing.	23
Table 2-4: Difference in head plumage colour scores of males and females in 18 individual pairs of gannets.	24
Table 2-5: Recommendations for the best use of gannet sexing techniques.	28
Table 3-1: Duration of nest attendance periods and percentage of total time spent at the nest by male and female gannets during chick-rearing.	37
Table 3-2: Percentage of time with neither parent present at the nest in relation to hatching date and fledging success.	39
Table 3-3: Equitability of foraging and nest attendance of males and females in relation to fledging success and chick hatching date.	40

Chapter 1

General Introduction



Different species of birds exhibit a wide range of mating systems from polygyny (males have more than one female partner) to polyandry (females have more than one male partner; Lack 1968; Black 1996). Polygyny occurs where females are clumped into groups (female defence polygyny), or where the resources needed to raise several broods of offspring are located in a position that can be defended and monopolised by one male (resource defence polygyny; Black 1996). When there is no such control of resources or females, polygyny can still occur where males order themselves in a hierarchical structure, where females can then choose partners based on male social status (male dominance polygyny). Lekking is one example of this last type of polygyny (Alatalo *et al.* 1996).

In polyandrous species, the female is freed from the responsibility of caring for the offspring, so can then lay several more clutches with different males. In birds, this strategy is uncommon, but the mechanisms that promote this strategy are essentially similar to those found in polygyny: females defend resources necessary to males (resource defence polyandry), females are loosely gregarious, mating with several males, then leaving them to care for the offspring (male defence polyandry), or females defend access to males (male access polyandry; Emlen and Oring 1977; Gowaty 1996).

Although a number of species show various forms of polygamy, monogamy is the most common mating system in birds, occurring in over 90% of all species (Lack 1968). Monogamy is found in systems where there is no environmental

“polygamy potential” (Emlen and Oring 1977), or when individuals have no opportunity to take advantage of any such potential (Gowaty 1996). For instance, Veiga (1992) found that male House Sparrows (*Passer montanus*) were normally monogamous, but would defend more nests than usual when nest boxes were artificially supplied. However in spite of this, male pairing success did not increase. Thus, the availability of other resources such as food may have limited males to a single partner (Gowaty 1996).

In many species, the level of care required to successfully rear young is substantial, and requires input from both parents. If males of these species were to put energy into other offspring with a different mate, the costs in terms of reduced offspring survival may outweigh the benefits in terms of extra-pair paternity. Gowaty (1996) separated monogamy into two distinct categories: social monogamy and genetic monogamy. In social monogamy, there is usually, but not always some level of bi-parental care involved, parents may co-operate in raising the offspring, and socially monogamous pairs may or may not engage in extra-pair fertilisations. Genetic monogamy is defined as a system where extra-pair fertilisation does not occur, making the offspring raised genetically related to both parents.

Within both forms of monogamy there is potential for conflict to arise between breeding partners in terms of the amount of care each partner is willing to give to their offspring (Trivers 1972), and between parents and offspring in terms of the

levels of provisioning demanded by chicks and provided by parents (Parker and Mock 1987). Individual fitness is described in terms of the total number of offspring produced in one's lifetime, and this number can be affected by the amount of parental care given by an individual's partner. The more care given by one parent, the less care it is necessary for its partner to give. On the other hand, the lower the effort made by one parent, the greater the input must be by its partner. Mathematical modelling of the interactions between the two parents suggests that the effort that each partner actually exerts is an evolutionary stable state (Chase 1980; Houston and Davies 1985) in which both parents give the minimum amount of effort necessary to achieve reproductive success each year. These models successfully predicted the contribution made towards chick-rearing by male and female Dunnocks (*Prunella modularis*; Houston and Davies 1985). However, in long-lived species, where pair bonds are maintained over more than one breeding season, this model fails to include the possible influence that the input of one parent has on the input of its partner in successive breeding events. This may be an important omission, particularly if a low input from one parent leads to divorce (Grant and Grant 1987; Linden 1991).

Because females make a larger initial investment than males in reproduction, due to larger gamete size, they have more to lose if the offspring fails because they will have to invest more energy than males to produce another gamete, and they therefore may make a larger investment throughout the remainder of the reproductive period (Orlans 1969; Trivers 1972). In contrast, males of several

monogamous species make larger contributions than females to territory defence and nest building, and this may balance the initial unequal investment in gametes prior to egg-laying (Montevecchi and Porter 1980; Burger 1986). In these species, males and females might be expected to contribute equally to later stages of reproduction.

Most research on the contribution of males and females to rearing offspring has focused on interactions between partners in short-lived species (Arcese 1989; Veiga 1992; Blondel *et al.* 2000), while relatively little work has examined long-lived monogamous species with long-term pair-bonds (Black *et al.* 1996; Sydeman *et al.* 1996). Further data are required to determine how the contributions of males and females to rearing offspring are determined in such species.

1.1 Seabird Life Histories

Seabirds spend at least part of their life around the sea, and nest on offshore islands or in coastal regions (Furness and Monaghan 1987). They include members of the Orders Procellariiformes (Albatrosses, Fulmars, Shearwaters and Petrels), Sphenisciformes (Penguins), Pelecaniformes (Pelicans, Boobies, Gannets, Frigatebirds, Tropicbirds and Cormorants) and Charadriiformes (Skuas, Gulls, Terns, Skimmers and Auks; Jonsson 1993). Seabirds are long-lived species (up to 60 years in the larger albatross species; Cramp 1985), with delayed

reproductive maturity (from 2-3 years in tropicbirds, gulls and some terns to 8-12 years in albatrosses, petrels and possibly frigatebirds; Furness and Monaghan 1987; Hamer *et al.* in press). They lay small clutches (generally 1-4 eggs; Nelson 1964) and have long breeding seasons.

Seabirds are generally socially monogamous with few examples of polygynous or polyandrous breeding systems. There is some evidence of female-female pairings in several species of gulls and terns, where females may share one male or achieve insemination through extra pair copulations (Ryder and Somppi 1979; Nisbet and Hatch 1999). Additionally, polyandrous systems, with one female pairing with several males, have been recorded in Brown Skuas (*Catharacta antarctica*; Young 1978). There is no evidence of co-operative breeding in seabirds, although, adoption of nonfilial young by foster parents has been recorded in several species of gulls and terns (Saino *et al.* 1994; Bukacinski *et al.* 2000), and in Thick-billed Murres (*Uria lomui*; Gaston *et al.* 1995). This adoption is generally instigated by the chick, which has left its nest probably because of being poorly fed. Foster parents can reject the chicks resulting in infanticide, but only at the risk of killing their own offspring (Brown 1998), so they generally accept and feed the chick. Additionally, fostering might also increase the fitness of an individual if foster-parents and foster-chicks are closely related (e.g. Common Gulls *Larus canus*; Bukacinski *et al.* 2000).

Foraging for food for offspring is an important component of parental investment in non-precocial seabirds. As central place foragers, these species undertake long foraging trips to collect food, and then return to the nest site to deliver food to their chicks (Orians and Pearson 1979). Most previous studies of food provisioning in seabirds have not examined males and females separately, and those that have done so have been largely restricted to sexually size dimorphic species (Weimerskirch *et al.* 1997; Erikstad *et al.* 1998; Gonzalez-Solis *et al.* 2000). Some such studies have recorded different contributions to food provisioning by males and females, possibly resulting from separation of foraging grounds (Hatch 1990; Gonzalez-Solis *et al.* 2000). However, very little research has examined possible differences between sexes in the roles of provisioning in species with negligible sexual size dimorphism (Gray and Hamer in press.).

Long-lived, iteroparous species such as seabirds would be expected to limit their current reproductive investment so as not to compromise future reproductive output (Drent and Daan 1980). In seabirds individuals might be expected to reduce their work rate to the minimum level required to successfully raise offspring, and their partner might be expected to do the same (Chase 1980). However, some studies have shown that breeding success is related to equitability in investment between breeding partners (Croxall and Ricketts 1983; Burger 1986), meaning that pairs are more successful when both parents do an equal amount of work. Equitability of investment between partners is especially relevant for long-lived seabirds because pairs will potentially raise many offspring

together over several breeding seasons. However, few studies have examined this question and further data are required to determine the importance of equitability between partners in different species of seabirds.

1.2 Northern Gannets

Northern Gannets (*Morus bassanus*; here termed gannets) are in the Order Pelecaniformes. Their geographical range includes the North Atlantic Ocean up to the arctic fringe with non-breeders and immature birds found as far south as the fringe of the tropics (Cramp 1985). They exploit cold, nutrient-rich waters, and rely on seasonally abundant fish stocks including herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). Gannets capture fish by plunge diving (Garthe *et al.* 2000), a strategy shared with other Pelecaniformes such as the Brown Booby (*Sula leucogaster*; Anderson *et al.* 1991).

Gannets become reproductively active between 4 and 7 years of age (Nelson 1978). They have an extended breeding season, from February to October, with breeding adults returning to the colony about 6-8 weeks prior to egg-laying to defend territories and begin re-building nest sites. Pairs incubate their egg for six weeks, and care for their chick at the nest for about 13 weeks before fledging. Parents travel long distances (up to 500 km) away from the breeding colony during foraging trips (Hamer *et al.* 2000), and the protracted breeding season of

gannets is typical of the slow growth patterns found in many pelagic seabirds (Goodman 1974).

Gannets lay one egg per clutch, and this egg is only 3.6% of the female's body mass (Ricklefs and Montevecchi 1979), which is one of the smallest egg to female mass ratios of all birds (Ricklefs 1977). If the egg is lost early in incubation, females usually re-lay within three weeks (Nelson 1978). Both members of the pair participate in incubation. Gannets do not have a brood patch, but achieve incubation by placing their webbed feet over the egg. Their feet are highly veined and produce sufficient heat to maintain egg temperature. This method of incubation does not appear to hinder the ability of individuals to incubate more than one egg at a time because boobies also use this incubation technique, and Peruvian Boobies (*Sula variegata*) lay up to four eggs per clutch (Nelson 1978). Hatching and fledging success are usually high in gannets compared to many other species of seabird (Nelson 1978; Montevecchi and Porter 1980).

In gannets, as in most seabirds, both sexes feed the chick. Paramount to understanding the food provisioning strategies of parents is determining the partitioning of duties within a pair (Chase 1980; Drent and Daan 1980). Until recently it has been very difficult to examine sexual differences in foraging and nest attendance behaviour of gannets because of the similarity in appearance of males and females. The advent of molecular DNA sexing (Griffiths *et al.* 1998) has recently enabled the determination of sex in such species without the need for

internal examination (Baker *et al.* 1999; Jodice *et al.* 2000), but this technique has not previously been applied to gannets.

1.3 The Study Site

This study was carried out at Great Saltee Island (52° 8' 30" N. 6° 41' W.), five kilometres south of Kilmore Quay, County Wexford, Ireland (Fig. 1-1). The island is privately owned and is not permanently inhabited, but large numbers of tourists visit on a daily basis.

In addition to gannets, several other seabird species nest on Gt. Saltee, including Manx Shearwaters (*Puffinus puffinus*), Puffins (*Fratercula arctica*), Guillemots (*Uria aalge*), Fulmars (*Fulmarus glacialis*), Kittiwakes (*Rissa tridactyla*), Razorbills (*Alca torda*), Shags (*Phalacrocorax aristotelis*), Great Black-backed Gulls (*Larus marinus*), Lesser Black-backed Gulls (*Larus fuscus*) and Herring Gulls (*Larus argentatus*). Gannets first bred at Great Saltee in 1929, and the population on the island is currently increase at a rate of c.a. 10% per anum (Thompson *et al.* 1998). There are two main gannetries on the island with 2000+ nesting pairs (Fig. 1-2). The smaller of the two, the Makestone Rock is located 20 metres off the shoreline of the island. The larger gannetry, where this study was conducted, is on the south-eastern tip of the island. The birds here tend to nest on rocky outcrops, and they mainly use Sea Campion (*Silene maritime*) gathered from the island to build their nests.

1.4 Aims and Objectives

In this thesis, I test the accuracy of different techniques for sexing gannets by comparing behavioural and morphological characteristics to DNA-based sexing (*Chapter 2*). In *Chapter 3*, I determine how the foraging trip durations and nest attendance patterns of males and females vary in relation to chick age. In *Chapter 4*, I discuss the results of my work in the context of seabird mating systems, and the possibilities for further research in this field.

Figure 1-1: Location of Great Saltee Island, Ireland

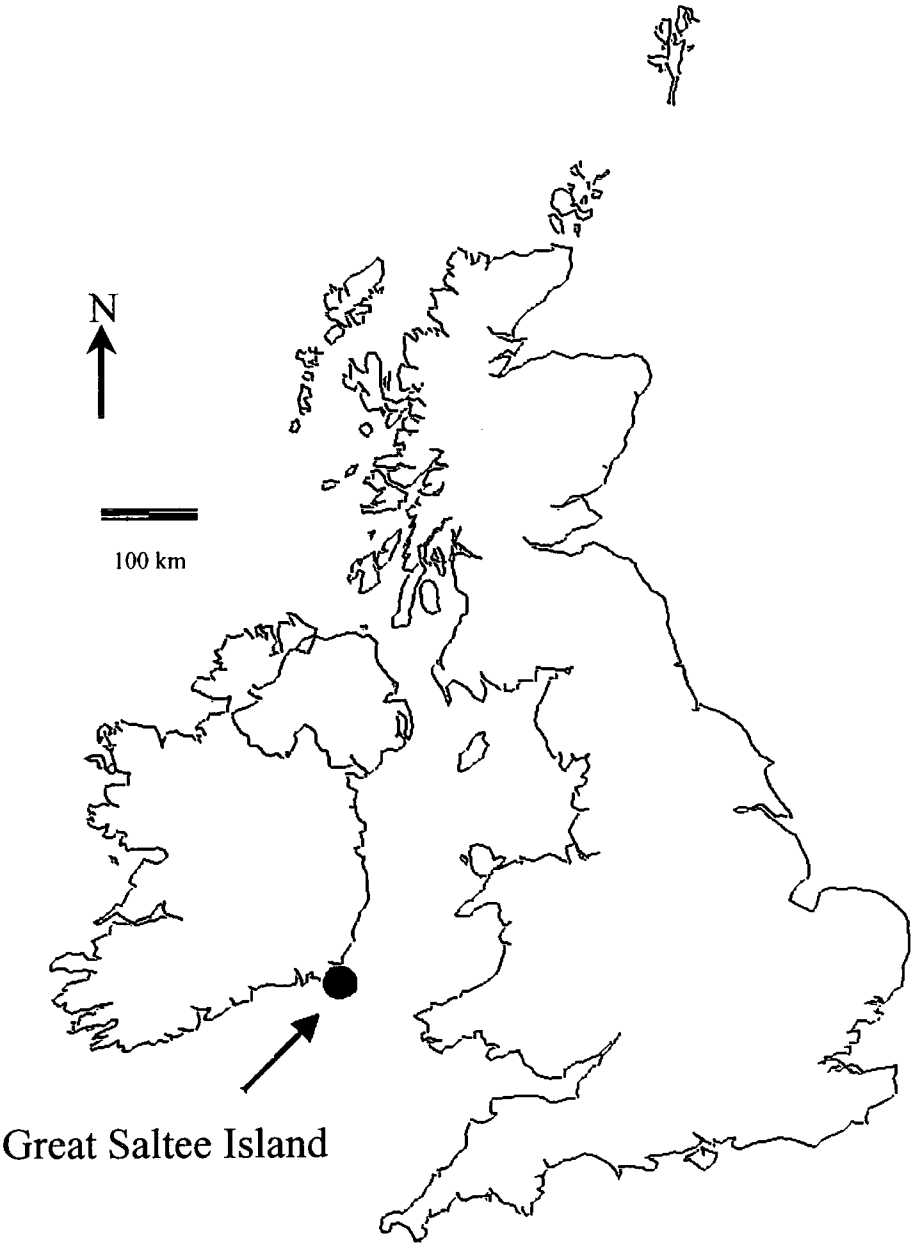


Figure 1-2: Map of Great Saltee Island, Ireland with notation of the two gannet colonies.

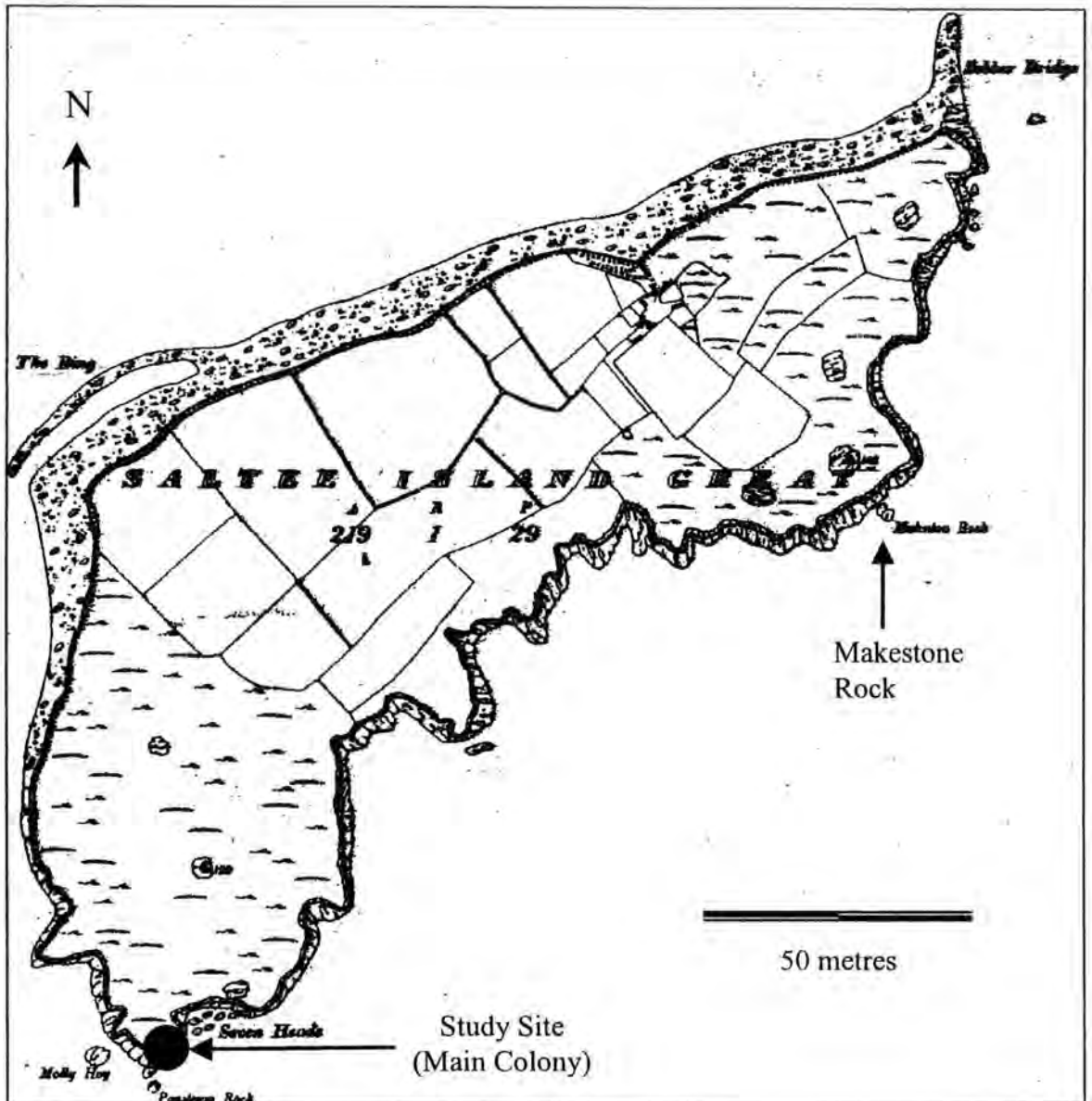


Photo provided care of Oscar Merne

Chapter 2

Sexing Gannets

by DNA, Behaviour and Morphology

2.1 Introduction

Differentiation of sex in a species is fundamental to understanding differences in behaviour and breeding ecology of males and females, but is problematic in many species of birds where the sexes appear similar in terms of plumage and soft-tissue colouration. In some cases, individuals can be sexed without the need for internal examination, during reproductive behaviours such as courtship feeding and copulation (Ellegren and Sheldon 1997), from external morphological measurements either singly or combined in a multivariate discriminant analysis (Klecka 1980) or, shortly after egg laying, from cloacal examination (Boersma and Davies 1987; Gray and Hamer in press). Different techniques are unlikely, however, to provide the same degree of accuracy, or even be possible for any one species. There is thus a need to determine the applicability and accuracy of each potential technique for different species.

On first inspection, gannets appear sexually monomorphic with no obvious difference between males and females in body size or plumage. However, it has been suggested that there are morphological and behavioural differences between the sexes and these are described below:

1. Males may have wider and shorter bills than females.

2. Head plumage colouration is deep yellow with orange-brown overtones in both sexes at the start of the breeding season, but may fade progressively in females to pale yellow spotted with white by the end of chick-rearing.
3. Gannets' feet and legs are black with coloured lines running along the tops of the toes and up the tarsi. These lines are present in all adults and may tend towards turquoise in females and green in males.
4. When one member of the pair returns to the nest the male may vigorously bite the nape of the female.
5. Collection of nest material can occur at any stage of the breeding season and is believed to be carried out mainly by males.

These characters have been used to sex individuals of this species in the past (Nelson 1965, 1978; Montevecchi and Porter 1980), but there has yet to be a quantitative evaluation of their accuracy or applicability for determining sex. Molecular genetic techniques now permit unequivocal determination of sex from nuclear DNA in blood and other tissues (Ellegren and Sheldon 1997; Griffiths *et al.* 1998; Lessells and Mateman 1998), providing the opportunity to accurately assess the value of other techniques for differentiating males and females (Griffiths *et al.* 1992; Griffiths and Tiwari 1995; Baker *et al.* 1999; Jodice *et al.*

2000). The aim of this study was therefore to use DNA-based genetic techniques to determine the sexes of adults unequivocally, to use this information to evaluate a range of other techniques for sex determination and to review the benefits and limitations of each technique for gannets and for other species of birds.

2.2 Methods

Breeding adult gannets were caught at the nest shortly after chick-hatching with a roach pole fitted with a brass noose. No attempt was made to trap birds during incubation because of the high likelihood of egg loss. A small sample of blood (<1 ml) was taken under licence from the tarsal vein, using a separate needle and syringe for each bird. Sex identification is based on amplifying a portion of two semi-linked genes: (1) CHD-Z, which is on the Z-chromosome, is common to both sexes and forms a positive control; (2) CHD-W, which is on the female-specific W chromosome and is used to identify sex. Blood samples were stored at room temperature in 95% alcohol and subsequently analysed at Glasgow University, UK using methods described by Griffiths *et al.* (1998). Blood was centrifuged to remove the plasma, and DNA was then extracted from red blood cells. The CHD-W and CHD-Z genes located on the avian sex chromosomes were amplified using P2 and P8 primers and gel electrophoresis of the PCR products was then used to reveal the presence of a single band, representing a male, or a double band, representing a female. All samples were analysed without knowledge of the suspected sex of the bird based on behaviour and morphology.

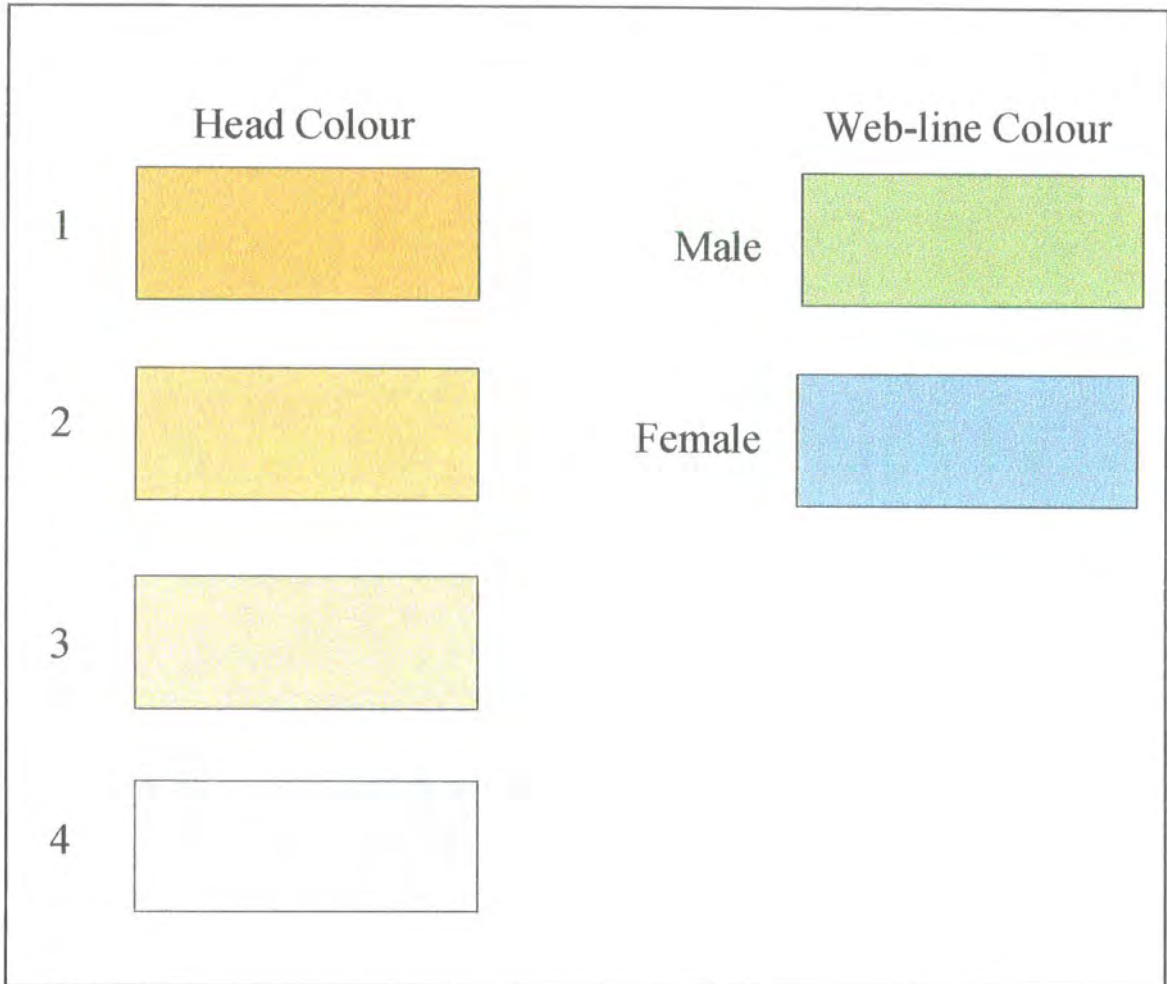
The following measurements were recorded for each individual captured: bill length (from the feather edge at the top of the bill to the most distant part of the curved end of the bill), bill width (at the base of the bill) and bill depth (at the base of the bill) to the nearest 1 mm using Vernier callipers; wing length (maximum flattened chord, from the carpal joint to the tip of the longest primary feather) to the nearest 1 cm with a slotted ruler; and body weight to the nearest 25 g with a 5 kg Salter balance. Differences between sexes were examined for each character separately and characters were then combined in a step-wise discriminant analysis (Norusis 2000).

Every bird captured was fitted with a red darvic ring with a unique sequence of three white engraved numbers on the left leg, and with a BTO ring on the right leg. Processing took no more than 10 minutes after which birds were released back to the nest. Marked individuals and their partners were then observed for a total of 415 hours covering all times of day (0400 – 2300 h) throughout the chick-rearing period (1 May – 15 August, 2000) from a hide approximately 30 metres from the study colony. The sexes of birds were not known from genetic analysis during observations. Morphological characters (head plumage and web-line colouration) and sex specific behaviours (nape-biting and gathering of nest material) were recorded at intervals of 5 - 10 days. Morphological characters were recorded only when both birds were present at the nest. Head plumage colours

were recorded on a scale from 1 (darkest) to 4 (lightest) by reference to a standard colour chart. Web-line colours were similarly assessed by reference to a standard chart (Plate 2-1). In recording nape-biting, only vigorous biting was included, to avoid possible confusion with fencing (Nelson 1978) or with incidental placement of the bill near the rear of the partner's head. Collection of nest material was recorded only when a bird arrived with material from outside the colony, and not when a bird gathered nest material from its immediate vicinity.

To examine how the accuracy of each character for sexing birds changed during chick-rearing, the 15-week observation period was divided into early (May 1 – June 8), middle (June 9 – July 12), and late (July 13 – August 12) chick-rearing and data were analysed separately for each period.

Plate 2-1: Example of the chart used in observations to obtain consistency in head and web-line colour assessment.



2.3 Results

2.3.1 Biometrics

In total 18 birds were measured (11 males plus seven females), all at separate nests. All body measurements were normally distributed (Table 2-1:

Kolmogorov-Smirnov one-sample tests, $P > 0.05$ for all measurements), and all except body mass had equal variance in males and females (Levene's test for equality of variances; $P > 0.3$ in all cases). Body mass was significantly more variable in females than males ($F_{1,16} = 11.2$, $P < 0.01$). All measurements had equal means in the two sexes (Table 2-1: t-tests using appropriate variance estimates; $P > 0.2$ in all cases). In a discriminant analysis, no variables were considered to be valid for inclusion in the classification function ($P > 0.1$ for improvement in model in all cases), and when the analysis was forced, 11 individuals were correctly classified (58%), which was no different from the proportion expected by chance (50%; $\chi^2_1 = 0.4$, $P > 0.05$).

Table 2-1: Morphometric data for gannets on Great Saltee Island.

	<i>Male (n=11)</i>			<i>Female (n=7)</i>		
	Mean	S.D.	Range	Mean	S.D.	Range
Bill length (mm)	97.3	4.0	12.3	97.2	3.0	9.6
Bill width (mm)	27.0	1.5	5.0	27.1	1.0	3.0
Bill depth (mm)	35.4	1.2	3.6	35.8	1.9	5.9
Wing (mm)	492.4	7.5	27.0	494.1	7.6	22.0
Weight (kg)	2.8	0.2	0.5	3.0	0.3	0.7

2.3.2 Morphology and Behaviour

There were 18 nests with at least one parent individually marked and of known sex from DNA analysis. I was able to assign sexes to birds at all these nests from nape-biting behaviour, but at <100% of nests from all other characters (Table 2-2). This was either because the two members of the pair were indistinguishable in terms of head plumage or web-line colour, or because nest-material collection was never observed at some nests.

Table 2-2: Effectiveness of four techniques for sexing gannets.

<i>Sexing Technique</i>	<i>% of nests where assignment possible</i>	<i>% correct when assignment possible</i>	<i>% correct overall</i>
Head colour	77.8	85.7	66.7
Web-line colour	44.4	62.5	27.8
Nape biting	100.0	100.0	100.0
Nest mat. collection	33.3	83.3	27.8

Nape biting occurred on 109 of 134 occasions when a bird returned to the nest (81%) and on all but one occasion it was performed by the male. Overall, males were significantly more likely to perform nape-biting when they returned to the nest (87 of 92 occasions = 95%) than when the female returned (21 of 41 occasions = 51%; $\chi^2_1 = 40.3$, $P < 0.001$). Where it was possible to assign sexes to birds, nape-biting behaviour was completely accurate, and both head plumage

colour and nest-material collection were reasonably accurate in assigning sex (Table 2-2). However, whereas it was possible to sex all birds correctly from nape-biting behaviour, only two-thirds of birds overall were sexed correctly from head plumage colour and <30% from the other two criteria (Table 2-2).

2.3.3 Seasonal Variation

The occurrence of nape-biting did not change during the chick-rearing period (23 of 28 returns = 82.1%; 39 of 49 returns = 79.6%; 47 of 57 returns = 82.5% in early middle and late chick-rearing respectively; $\chi^2_2 = 0.02$, $P = 0.99$). There was also no variation in the ability to sex birds from nape-biting behaviour at different stages of chick-rearing (Table 2-3; but N.B. the occurrence of frequencies of zero at all three stages of chick-rearing precluded statistical analysis of these data using χ^2 -tests).

Table 2-3: The ability of different techniques to sex gannets at different stages of chick-rearing.

Sexing Technique	Early			Middle			Late		
	correct	incorrect	unassigned	correct	incorrect	unassigned	correct	incorrect	unassigned
Head colour	8	1	9	10	2	6	10	2	6
Web-line colour	2	1	15	6	0	12	4	2	12
Nape-biting	17	1	0	17	0	1	18	0	0
Nest material	1	1	16	5	1	12	0	0	18

Figures in Table are numbers of nests in each category.

Males had darker head plumage than females on average at all stages of chick-rearing (males, median score = 2.3, IQR \pm 0.6; females, median score = 3.1, IQR \pm 0.6; Wilcoxon signed ranks test: $Z_1 = 2.8$, $n = 18$, $P = 0.005$). This difference became significantly greater as the season progressed (Table 2-4; Page test; Siegel 1956: $K = 3.0$, $n = 18$, $P = 0.001$). However, there was no change in the ability to sex individuals by head colour (Table 2-3: χ^2 -test with incorrect and unassigned nests combined; $\chi^2_2 = 0.2$, $P > 0.5$), or web-line colour (Table 2-3: $\chi^2_2 = 0.2$, $P > 0.5$) during the season.

Table 2-4: Difference in head plumage colour scores of males and females in 18 individual pairs of gannets.

<i>Stage of chick-rearing</i>	<i>Difference in head plumage score</i>	
	median	IQR
Early	2	1
Middle	2	1
Late	2.5	1.2

2.4 Discussion

DNA analysis has not previously been used to sex gannets, but it has been comprehensively tested (Griffiths *et al.* 1998) and it has independently been used

successfully to sex individuals from several species of birds including Starlings (*Sturnus vulgaris*; Griffiths *et al.* 1992), Purple Swamphens (*Porphyrio porphyrio*; Millar *et al.* 1996), Red Knot (*Calidris canutus*; Baker *et al.* 1999), Black-legged Kittiwakes (*Rissa tridactyla*; Jodice *et al.* 2000) and Guillemot (*Uria aalge*; Birkhead *et al.* 2001). Jodice *et al.* (2000) found that genetic analysis was not completely accurate, when compared with internal examination, in sexing Black-legged Kittiwakes (*Rissa tridactyla*). However, fewer than 3% of birds were sexed incorrectly and these errors were probably due to mislabelling of specimens in the field (Jodice *et al.* 2000). I am therefore confident that DNA analysis was able to correctly sex gannets in this study.

The highly conserved nature of biometric measurements makes them an effective sexing technique in dimorphic species. In these cases discriminant analysis can be a powerful tool in separating individuals. For example, Shy albatross (*Diomedea cauta cauta*) were sexed correctly in 98% of cases where both members of a pair were compared for sex (Hedd *et al.* 1998). For monomorphic species, like gannets, biometric measurements are much less reliable. Nelson (1978) found that male and female gannets on the Bass Rock, Scotland differed in bill length, width, and depth, although there was considerable overlap between sexes. On Great Saltee, there was a large amount of overlap between males and females in all five biometrics measured, resulting in no difference between sexes in any of these measurements. Geographical differences in morphology are possible explanations

for this discrepancy between the two different colonies. For instance, Baker *et al.* (1999) found a difference in biometric measurements of Red Knots over different geographic regions. It is also possible that in this study, within-observer variation in measurements was greater than between-sex variation. This could be tested using repeated measurement from individual birds (e.g. Barrett *et al.* 1989), although this would increase the processing time for each bird. The absence of any differences in the current study could also be attributable to the small sample sizes, although the differences between males and females in all three bill measurements were <1.5% of the mean (Table 2-1).

In contrast to using biometrics, gannets at Great Saltee could be reliably sexed from external colouration and behaviour, especially the latter (Table 2-2). These data indicate that some of the previously identified sex-specific characters of gannets (Nelson 1978; Montevecchi and Porter 1980) can be used as reliable indicators of a bird's sex. In particular, the performance of nape-biting was as reliable as DNA-based sexing at all stages of chick-rearing. Some females do very occasionally perform nape-biting, but even this small rate of error can be avoided if birds are sexed on the basis of several observations of nape-biting. In this context, nape biting occurs during most change-overs in adult attendance at the nest and so can be recorded relatively quickly. Collection of nest material is also a reliable indicator of sex but it is not as accurate as nape biting (Table 2-2).

Moreover, it occurs relatively infrequently, and only very rarely during early or late chick-rearing (Table 2-3).

Birds could be sexed fairly accurately from differences in head plumage colour when said differences were apparent. However, partners at > 20% of nests did not differ in head plumage colour at any stage of chick-rearing (Table 2-2). While there was no evidence that the accuracy of this technique increased through the season, there was a significant increase in the difference between male and female head colours as the season progressed (Table 2-4). This increasing difference makes differentiation between the pair at the nest much easier later in the season. While it is possible to measure the difference between individuals throughout the breeding season, I would recommend using head colour difference only when chicks are six weeks post-hatching.

Web-line colour was the least effective of all methods tested. The low percentage of nests where assignment was possible (44%), in conjunction with the low accuracy of the technique (63%) meant that only 28% of all nests were correctly sexed by web-line colour. The small number of nests where sex was recorded was in part due to the difficulty of observing gannets' feet, especially when pairs were together at the nest. See Table 2-5 for general recommendations for the use of each technique.

Table 2-5: Recommendations for the best use of gannet sexing techniques.

Sexing Technique	Recommendation
Nape Biting	100% accurate. Sound technique throughout the season.
Head Colour	Good technique to use in conjunction with nape biting. More reliable later in the season (chick age >6 weeks)
Nest Material Collection	Reliable when witnessed, but unpredictable occurrence
Biometrics	Not recommended
Web colour	Not recommended

Behaviour and head plumage colour is best suited for sexing gannets when each individual is marked in a way that allows for long term identification, such as with colour rings or dye. Otherwise, individual identity must be established at the beginning of each new observation period, introducing the possibility of incorrect identification. There is an annual chick-ringing program at Great Saltee, which meant that a large portion of the breeding population was ringed. However, this may not be the case at other colonies, especially where adults nest on inaccessible cliff-faces.

This study suggests that gannets can be accurately sexed using either behavioural or morphological characteristics. Assuming individuals are marked, morphology and DNA-analysis can be used to support behavioural observations, which seem to be the most easily obtained and accurate of the methods tested. However, the

sexing techniques used will be largely dictated by the individual circumstance of each project.

Chapter 3

Foraging and Nest Attendance Patterns of Males and Females

3.1 Introduction

Most birds (with the exception of megapodes; Jones and Birks 1992) provide some form of care for their offspring after hatching, and in non-precocial species, one or both adults travel between the nest site and foraging areas to obtain food for their chicks. The availability of food resources influences the type of breeding systems present in different species: in environments where food is abundant, polygamous breeding systems may develop where one individual can successfully raise the pair's offspring without the help of their mate. Conversely, when food is comparatively scarce or unpredictable, socially monogamous mating systems may develop, where both parents participate in raising their offspring (Emlen and Oring 1977).

Approximately 90% of all bird species are socially monogamous (Lack 1968), and in many cases this monogamy appears to reflect the need for bi-parental care, although each can in some circumstances occur without the other (Mock and Fujioka 1990; Gowaty 1996). Bi-parental care requires co-ordination between breeding partners (Houston and Davies 1985), however, there is a strong potential for sexual conflict to arise between partners over the contribution that each makes to the offspring (Trivers 1972; Parker 1979). Both mathematical models (e.g. Chase 1980; Houston and Davies 1985) and experimental manipulations of chicks and parents (Mock and Ploger 1987; Wolf *et al.* 1998) have indicated that parents often adjust their effort facultatively to that of their partner, and that parents are generally not working at maximum capacity (see Mock *et al.* 1996 for a review).

However, we are still not able to quantitatively predict the relative workloads of males and females in monogamous species, and this shortcoming is partly due to a lack of empirical evidence on the contributions of monogamous males and females to rearing offspring (Mock *et al.* 1996).

Most seabirds are socially monogamous with a high probability of retaining the same breeding partner from one year to the next (Mills *et al.* 1996; Wooller and Bradley 1996; Catry *et al.* 1997). To date, most studies of parental care in seabirds have focused on describing general patterns of food delivery (e.g. changes in meal size and feeding frequency during nestling growth; Hunter 1983; Weimerskirch *et al.* 1999). Further work has examined the interactions between parents and chicks (Ricklefs 1979; Hamer and Hill 1994; Weimerskirch *et al.* 1994; Phillips and Furness 1998; Weimerskirch 1998) and effects of parental experience and condition on growth and provisioning of chicks (Coulson 1966; Charlesworth and Leon 1976; Curio 1983; Hamer and Furness 1991; Croxall *et al.* 1992; Martin 1995; Jouventin *et al.* 1999; Wendeln and Becker 1999; Berrow *et al.* 2000). Yet comparatively few studies have examined the chick-rearing behaviours of males and females separately (Hunter 1984; Weimerskirch 1995; Gonzalez-Solis *et al.* 2000). Moreover, these studies have, in some cases, found differences between the sexes in their provisioning strategies, including separate foraging grounds (Gonzalez-Solis *et al.* 2000) and differences in foraging trip durations (Weimerskirch 1995) in some species. This research indicates a need for further data on the food provisioning behaviour of males and females from

other seabird species. Additionally, some studies have shown that equitability in the division of labour between partners increases the success of the pair (Croxall and Ricketts 1983; Burger 1986). However, more data are needed to understand the relationship between equitability and various aspects of breeding performance in other species. In particular, it is not clear whether high equitability is indicative of a high-quality or a well co-ordinated pair (in which case it might be expected to be correlated with other indices of quality such as relative hatching date; Coulson and Porter 1985), or whether high equitability itself results in higher breeding success (for instance if low equitability results in one partner leaving chicks unattended with a high risk of predation).

Gannets are socially monogamous seabirds whose single-egg clutches weigh only 3.6% of female body weight (Ricklefs and Montevicchi 1979). Chicks are altricial, hatching at a relatively early stage of development (Starck and Ricklefs 1998) and typically take 12-13 weeks from hatching to fledging (Nelson 1978). Adults have high mass-specific energy expenditure during foraging trips, resulting from an energetically expensive mode of flight coupled with a pursuit-diving mode of prey capture (Birt-Friesen *et al.* 1989; Garthe *et al.* 2000). Thus, provisioning of food for the chick is an important component of adults' annual energy budgets.

In this chapter I examine the foraging and nest attendance behaviour of gannets to determine if differences in provisioning behaviour exist between the sexes and

whether any such differences vary in relation to chick age. I also examine if hatching date and fledging success have any relationship with equitability of foraging and attendance patterns within pairs.

3.2 Methods

Data were collected only at nests where adults were easily distinguished from colour-rings or from one parent wearing a BTO ring. Adults at all these nests were sexed from DNA-analysis or from sex-specific morphology and behaviour (*Chapter 2*). These nests were observed over seven observation periods, each lasting 2-6 days (24 days in total) between 3 May (late incubation) and 14 August (late chick-rearing), 2000. Observations were made continuously throughout daylight hours (beginning 0400 - 0500h, ending 2200 - 2300h, depending on date) and arrival and departure times of individual birds were recorded to the nearest minute. Foraging trip durations were calculated as the time (minutes) elapsed between a bird departing and returning to its nest. Birds occasionally made short trips (< 30 minutes) after which the chick was not fed, and these were not included as foraging trips. Gannets sometimes make trips lasting 24 hours or longer (Nelson 1978; Hamer *et al.* 2000). Short observation periods (<2 days) will thus tend to miss the beginnings or ends of longer foraging trips, resulting in systematic under-recording of trip durations. However, in this study, recorded trips did not differ in length between observation periods of two and six days (mean for 2 - day observations = 12.8 h S.D. \pm 8.9, mean for 6 - day observations

= 13.5 h S.D. \pm 6.2; paired t-test: $t_{10} = 0.9$, $P = 0.4$), and so I am confident that these data permitted accurate calculation of trip durations.

There is generally very little activity in gannet colonies overnight (Nelson 1978). However, on five occasions in this study (1% of total departures), individuals left their nest site unattended at some point during the night, and these birds were each assumed to have left immediately after the end of the previous day's observations. On no occasions did individuals arrive during the night.

During this study, data were collected repeatedly for many days from the same individual nests. To account for these repeated measures, the breeding season was divided into incubation plus four chick age-classes (1-4 weeks, 5-8 weeks, 9-12 weeks, >12 weeks). Data for each age-class were aggregated into a single mean value for each nest, and test statistics were calculated from aggregated mean values, following Sokal and Rohlf (1981). Direct observations of hatching were not made at most nests, so chick ages were estimated using criteria given by Nelson (1978) and Montevecchi and Porter (1980) based on feather development and motor coordination of chicks. Chicks not seen on the nest after they reached 12 weeks of age were assumed to have fledged. All data were normally distributed (as determined by Kolmogorov-Smirnov one-sample tests) except where otherwise stated.

3.3 Results

3.3.1 Nest Attendance

I recorded 212 periods of nest attendance over 618 nest-days at 38 nests. Data were collected at seven nests during late incubation and there was no difference in the proportion of time spent by males at these nests between incubation (mean = 0.53, S.D. \pm 0.21) and the first four weeks post-hatching (mean = 0.53, S.D. \pm 0.11; paired t-test using arcsine-transformed data: $t_6 = 0.03$, $P = 1.0$). Males spent a significantly larger proportion of time at the nest than females during chick rearing (53% and 42% respectively; Table 3-1: paired t-test using arcsine-transformed data; $t_{37} = 2.9$, $P = 0.01$). There was no difference between sexes in the durations of individual periods of attendance (Table 3-1; paired t-test: $t_{33} = 1.1$, $P = 0.3$; variation in sample sizes is due to two males and one female that did not undertake an entire nest attendance period during observations), but males returned to the nest more frequently and undertook significantly more nest attendance periods ($t_{33} = 2.6$, $P = 0.01$). The proportion of time spent at the nest by each sex did not change during chick-rearing (Fig. 3-1; Analysis of covariance with chick age-class as a covariate: $F_{1,167} = 0.9$, $P = 0.4$).

Table 3-1: Duration of nest attendance periods and percentage of total time spent at the nest by male and female gannets during chick-rearing.

	<i>Duration of nest attendance period</i>			<i>Proportion of time spent at nest (%)</i>		
	n	Mean	S.D.	n	Mean	S.D.
Male	35	16.0	5.3	38	53.1	13.2
Female	37	15.0	7.3	38	41.9	13.5

Males and females spent little time together at the nest overall ($0.9 \pm 0.1\%$ of the total observation period), but this proportion was significantly higher when chicks were >12 weeks old than at younger ages (Fig. 3-2: one-way ANOVA of arcsine transformed data followed by Fisher's LSD test: $F_{4,133} = 5.3$, $P = 0.001$).

3.3.2 Trip Durations

There was significant repeatability in foraging trip durations of individuals (ANOVA to measure intraclass correlation; Zar 1996: $F_{76, 312} = 1.7$, $r_i = 0.1$, $P < 0.01$). Trip durations during late incubation (mean = 21.8h S.D. \pm 12.3) were no different to those during the first four weeks post-hatching (mean = 19.2h S.D. \pm 10.4; paired t-test for mean trip durations at each nest: $t_{12} = 0.9$, $P = 0.4$; there were only 13 nests where trip durations were recorded for both incubation and the first four weeks post-hatching). Overall, average post-hatching foraging trips by

males were 4 – 28 hours, and those by females were 10 – 40 hours in duration (Fig. 3-3), and the distributions of trips by both sexes were normal (Kolomogorov-Smirnov test: for males; $Z = 0.7$, $n = 38$, $P = 0.7$, for females; $Z = 0.7$, $n = 38$, $P = 0.7$). Females made significantly longer trips (21.0 hours, $n = 38$, S.D. ± 8.4) than males (17.3 hours, $n = 38$, S.D. ± 8.2 ; Fig. 3-3: paired t-test: $t_{35} = 2.2$, $P = 0.03$; two nests were excluded from the analysis because trip durations were recorded for only one sex). Durations of foraging trips by males decreased with increasing chick age (Fig. 3-4; linear regression excluding data for incubation: $F_{1,74} = 6.5$, $P = 0.01$, $R^2 = 0.07$) according to the following equation:

$$\text{Trip duration (hours)} = -0.29 (\text{SE} \pm 1.1) \text{ Chick age (days)} + 21.67 (\text{SE} \pm 1.1)$$

In contrast, females did not change their foraging trip durations as chicks grew (Fig. 3-4: $F_{1,70} = 0.5$, $P = 0.5$).

3.3.3 Non-attendance

In total, 15 nests (40%) experienced some level of non-attendance by parents. The degree of non-attendance differed markedly between nests, from 0% to 39%, averaging 4.7 % (S.D. ± 1.3) of the total observation period. Non-parametric analysis was performed on the level of non-attendance at different nests because all attempts to normalise the data failed (Kolomogorov-Smirnov test: $Z = 4.4$, $n = 138$, $P < 0.001$). The proportion of time chicks were left unattended increased significantly with chick age (Fig. 3-5: Kruskal-Wallis one-way ANOVA: $H_3 =$

38.9, $P < 0.001$). However, there was no relationship between the total amount of non-attendance and hatching date (Table 3-2: Mann-Whitney $Z < 0.1$, $n = 30$, $P = 0.9$), or fledging success (Table 3-2: Mann-Whitney $Z < 1.0$, $n = 21$, $P = 1.0$; sample sizes are reduced because chicks at 17 nests had not fledged by the end of the study). Males left chicks unattended significantly more often than did females ($\chi^2_1 = 8.9$, $P = 0.02$): males left chicks unattended on 38 occasions whereas females did so on only 7 occasions. 15 nests were left unattended at least once. Of these, 14 were left unattended by males, whereas only five were left unattended by females, and this difference was significant ($\chi^2_1 = 4.05$, $P < 0.05$).

Table 3-2: Percentage of time with neither parent present at the nest in relation to hatching date and fledging success.

<i>Hatching Date</i>				<i>Fledging success</i>			
	Mean %	n	S.D.		Mean %	n	S.D.
Early Hatching	6.2	16	11.0	Fledged	6.1	8	9.7
Late Hatching	4.2	14	6.0	Failed	3.8	13	4.9

3.3.4 Equitability in foraging and nest attendance of males and females

To examine whether there was any relationship between timing of breeding or fledging success and equitability of trip durations and nest attendance of partners, I calculated an index of equitability for both trip duration and proportion of time spent at the nest. In both cases, the index was calculated for each nest as the difference between the mean values for male and female parents, expressed as a percentage of the mean value for both parents combined. There was no difference

between early and late hatching pairs in the equitability of foraging trip durations (Table 3-3; t-test: $t_{28} = 0.3$, $P = 0.7$), or in the equitability of the proportion of time spent at the nest (Table 3-3; t-test: $t_{28} = 0.3$, $P = 0.8$). In addition, fledging success was unrelated to equitability of trip durations (Table 3-3: $t_{19} = 0.4$, $P = 0.7$) or in the proportions in time spent at the nest (Table 3-3: $t_{19} = 0.9$, $P = 0.4$).

Table 3-3: Equitability of foraging and nest attendance of males and females in relation to fledging success and chick hatching date.

	<i>Fledged</i>			<i>Failed</i>			<i>Early hatching</i>			<i>Late hatching</i>		
	Mean	n	SD	Mean	n	SD	Mean	n	SD	Mean	n	SD
Foraging trips	50.5	8	44.6	43.2	13	45.7	35.2	16	50.3	41.0	14	44.5
Nest attendance	40.4	8	48.0	22.9	13	43.6	27.9	16	43.6	31.3	14	46.4

There was no correlation between equitability in foraging trip durations and the level of non-attendance at the nest (Pearson correlation: $r = 0.31$, $n = 30$, $P = 0.1$), between the equitability in foraging trip durations and the equitability in nest attendance ($r = 0.3$, $n = 30$, $P = 0.1$), or between the equitability in nest attendance and the level of non-attendance at the nest ($r = 0.3$, $n = 30$, $P = 0.2$).

Figure 3-1: Proportion of time (± 1 S.E.) spent at the nest by males (closed circles) and females (open circles) in relation to chick age.

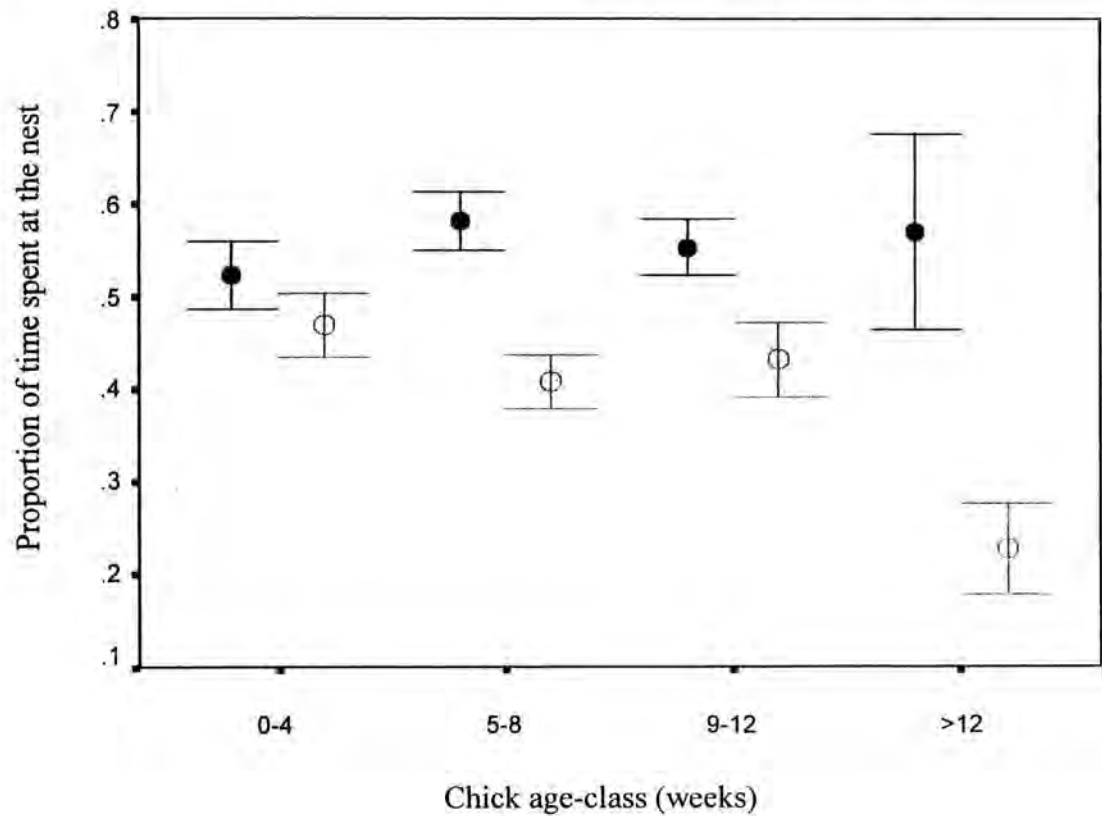


Figure 3-2: Percentage of time (± 1 S.E.) spent by parents together at the nest site in relation to chick age.

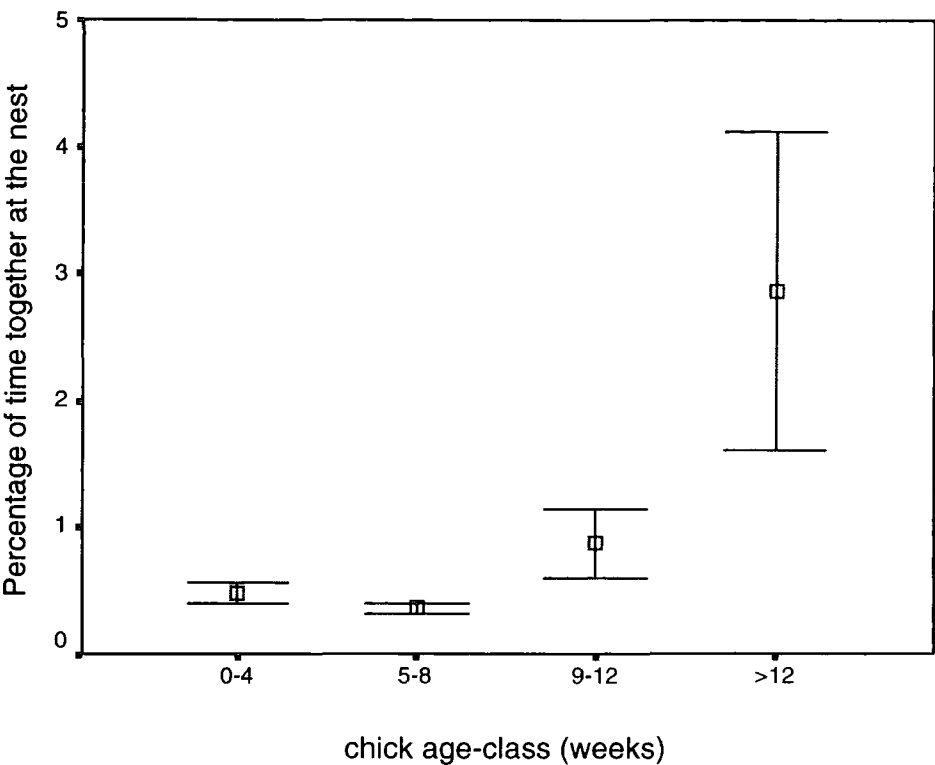


Figure 3-3: Frequency distribution of average foraging trip durations at each nest, for male (black) and female (white) gannets.

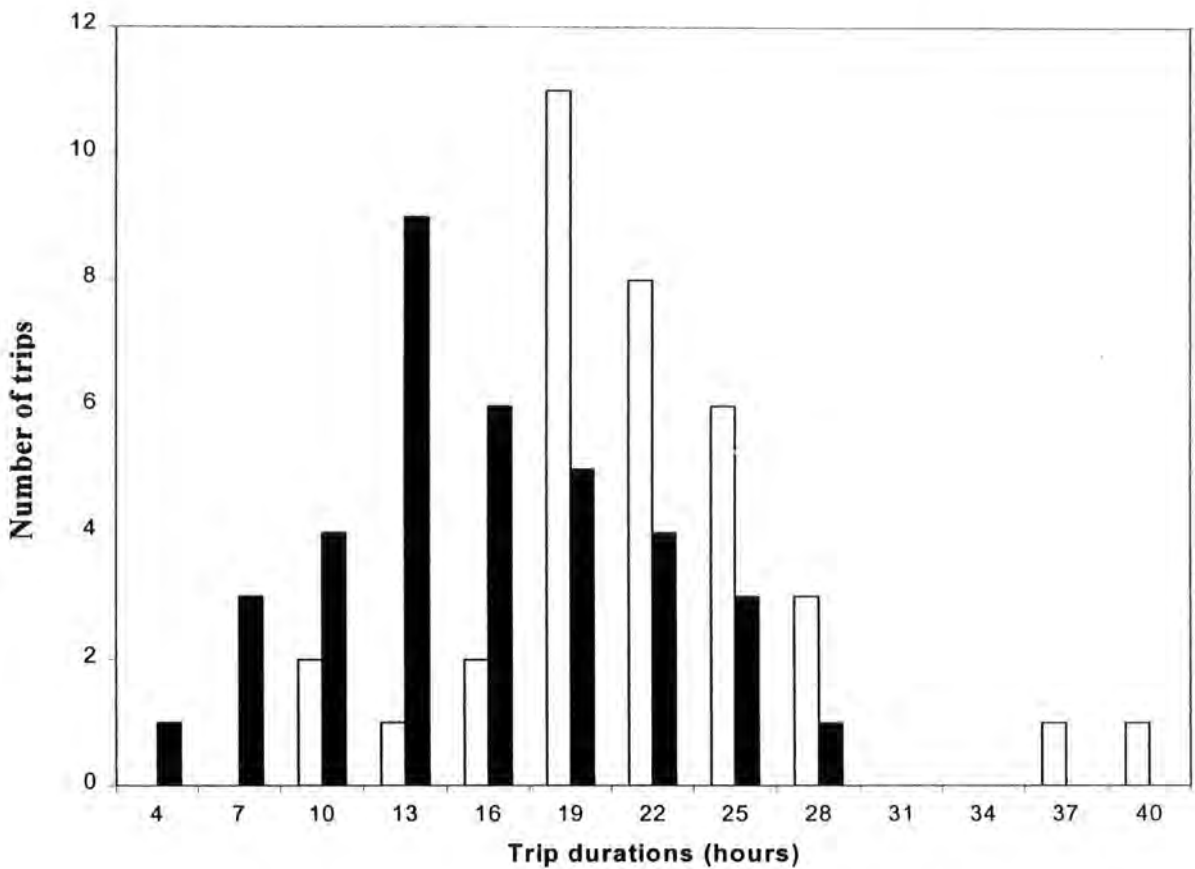
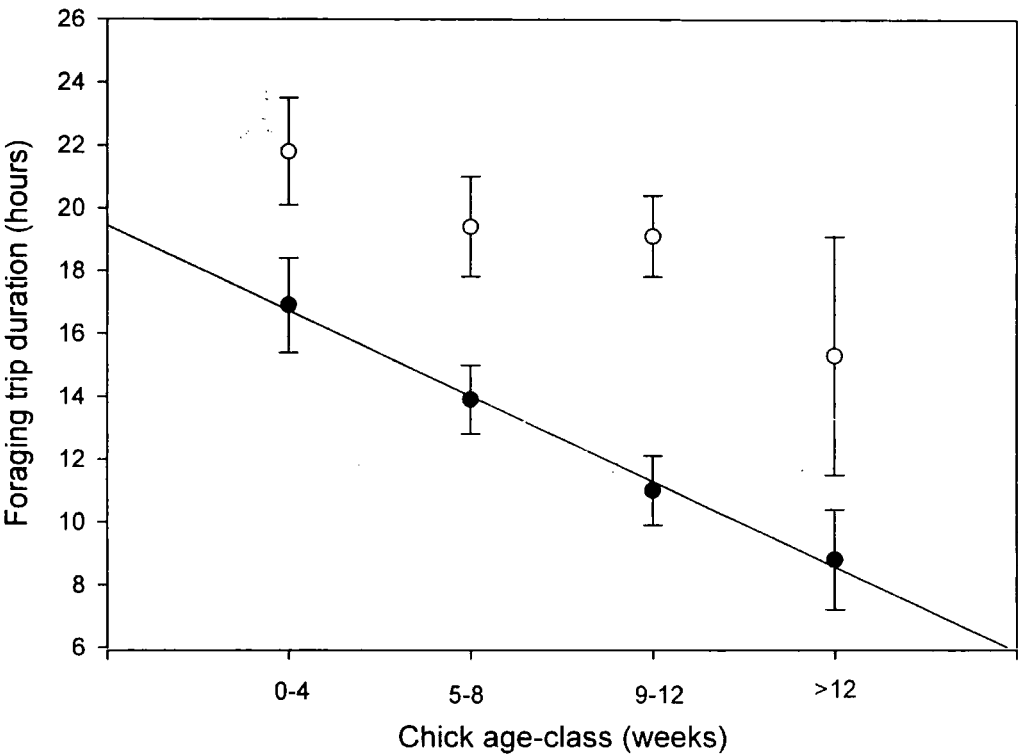
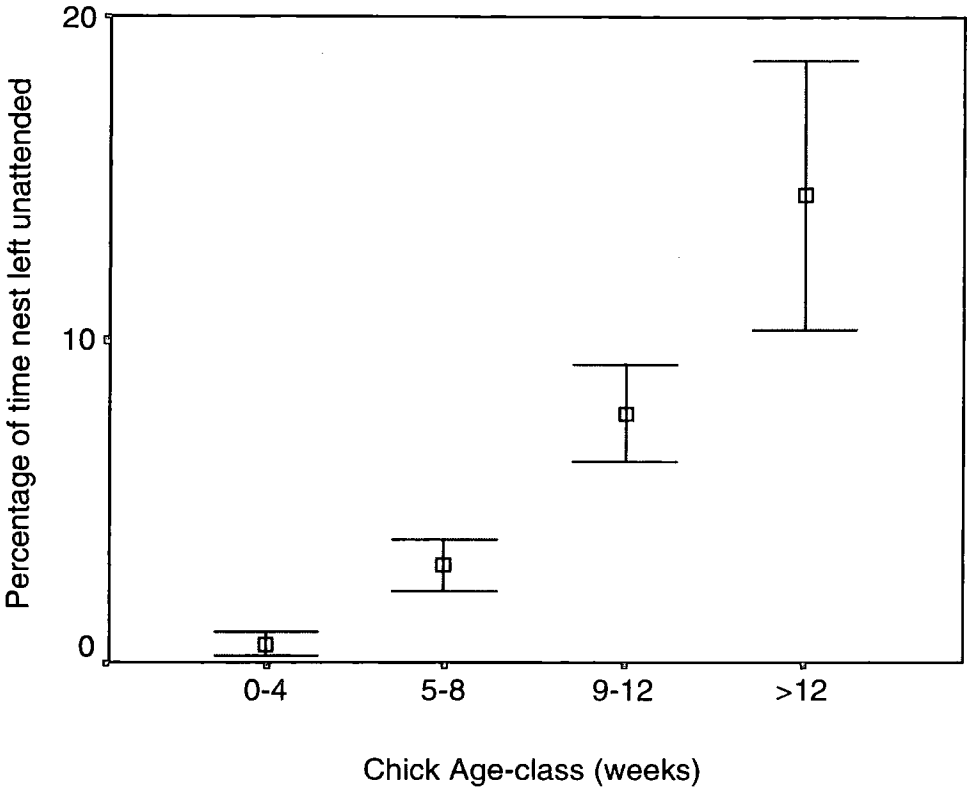


Figure 3-4: Foraging trip durations (± 1 S.E.) of male (solid circles) and female (open circles) gannets in relation to chick age.



The line represents the linear regression of male foraging trips on chick age-class ($R^2 = 0.1$). The regression was not significant for females.

Figure 3-5: Percentage of the total observation period (± 1 S.E.) when chicks were left unattended.



3.4 Discussion

3.4.1 Nest Attendance

Males spent a greater amount of time than females at the nest, largely as a result of returning more frequently and so performing more periods of nest attendance than females (Table 3-1). Males are primarily responsible for defending the nest site at the start of the breeding season (Nelson 1965, 1978) and in this study, non-breeding birds frequently challenged adults and attacked unattended chicks, presumably in an attempt to gain a breeding territory. Higher attendance by chick-rearing males than females could thus have been associated with nest defence. However, this hypothesis would predict a higher proportion of non-feeding visits by males, which was not the case (chicks were invariably fed at the end of foraging trips by both sexes).

A previous study of differences between male and female gannets at two colonies in Newfoundland found that females were at the nest longer than males during chick-rearing (Montevecchi and Porter 1980), while this study found the opposite, indicating a possible difference in male and female attendance patterns at two different colonies. The data from Newfoundland should, however, be viewed with caution because observation periods were limited to 1 - 16 hours, which may have been insufficient to accurately characterize nest attendance patterns (See methods).

3.4.2 Trip Durations

In several species of seabird (Weimerskirch 1995; Hunter 1984) the durations of foraging trips decrease towards the end of incubation, so that the attending bird has fresh food for the chick when it hatches. This pattern has also been recorded in gannets (Nelson 1978). On Great Saltee, there was no difference in trip durations during late incubation and brooding, possibly indicating that individuals had decreased the duration of foraging trips in order to be present with a fresh meal when their chick hatched. In several species of seabirds, adults deliver small feeds relatively frequently during the first few days post-hatching (Hamer and Hill 1997; Hamer *et al.* 1997), probably as a result of the small gut capacity of young chicks (Bolton 1995; Croxall *et al.* 1995; Phillips and Hamer 2000). There was no evidence for such a pattern in gannets. Instead, adults attending young chicks generally fed them small meals (as indicated by the time taken to transfer food from adult to chick) interspersed throughout their period of nest attendance, whereas older chicks were usually fed a single large meal shortly after the adult returned from foraging (pers. obs.; Nelson 1978). Feeding frequency then increased until fledging, as a result of a progressive shortening in durations of foraging trips by males (Fig. 3-4). This increase in feeding frequency presumably reflected the increasing nutritional requirements of growing chicks. Increases in feeding frequency during chick development have also been recorded in a number of other seabirds (Ainley and Schlatter 1972; Granadeiro *et al.* 2000) although in some pelagic species, feeding frequency does not increase with chick age (Hamer and Hill 1997; Phillips and Hamer 2000). The time parents spent together at the

nest increased when chicks were older than 12 weeks indicating that adults may have encouraged chicks to fledge by decreasing food delivery.

I present no information on the sizes of meals delivered to the nest. However as central place foragers, adults would be expected to respond to changes in chicks' nutritional requirement by altering return rates rather than payload (meal) size (Bolton 1995; Hamer and Thompson 1997; Granadeiro *et al.* 2000). There is also no difference between sexes in adult body mass (*Chapter 2*; Nelson 1978). The more frequent food delivery by males in this study thus probably resulted in a greater contribution by males towards food provisioning, especially among older chicks (Fig. 3-4).

Greater contributions to food provisioning by males have previously been recorded in some sexually size dimorphic species (Hunter 1984; Weimerskirch 1998) and appear to result from higher foraging efficiency in males, due to segregation of foraging grounds. For instance, in Giant Petrels (*Macronectes halli* and *M. giganteus*), males use their greater size to exclude females from feeding on carrion close to the nesting colonies (Hunter 1984). It is possible that gannets exhibit sexual segregation of foraging grounds, although this pattern has not previously been recorded in any sexually monomorphic species (but see Gray and Hamer *in press*). Hamer *et al.* (2000) found a strong relationship between foraging trip durations of gannets and distances travelled at sea. Thus, shorter trip durations of males could have resulted from them feeding closer to the colony.

Further examination of this question would require the use of satellite telemetry or some other means of following males and females at sea to determine feeding locations.

3.4.3 Non-Attendance

The proportion of time that chicks were left unattended increased with chick age (Fig. 3-5). This probably reflected the increasing nutritional requirements of growing chicks, coupled with a lower vulnerability of older chicks to attack by predators (such as Great Black-backed Gulls; *Larus marinus*) and by adult conspecifics. Males were more likely to leave chicks unattended than were females. The greater tendency of males to leave chicks unattended may be explained by males' higher attendance rates, but not entirely so: males were greater than five times more likely than females to leave chicks unattended, but males had much less than five times higher attendance rates.

Higher unattendance rates by males resulted from a greater disparity between mean trip durations of females and durations of attendance periods by males (21h and 16 h respectively) than between trip durations of males and durations of nest attendance periods by females (17 hours and 15 hours respectively). Coupled with higher rates of food delivery by males, this suggests that males may have traded off benefits of greater protection of chicks against benefits of greater food provisioning. An alternative explanation is that the longer foraging trips by

females sometimes exceeded the time that males were prepared to stay at the nest without foraging for themselves.

3.4.4 Equitability in foraging and nest attendance of males and females

Several studies have shown that pairs that lay their eggs earlier in the season tend to be consistently more successful than late layers (Martin 1987; Weimerskirch 1992; Wendeln and Becker 1999). Therefore, hatching date was used as an index of pair quality in this study. Pairs that hatched chicks earlier in the season, as well as pairs that successfully fledged chicks, showed no difference in the equitability of male and female foraging trip durations or nest attendance (Table 3-3) compared to pairs that hatched chicks later in the season or failed to fledge a chick. These data contrast with those for Herring Gulls (*Larus argentatus*) and Fulmars (*Fulmarus glacialis*), which indicated differences in equitability between more and less successful pairs (Burger 1986; Hatch 1990). This might suggest that equitability is relatively unimportant for successful reproduction in gannets. However, equitability could be operating at a finer scale than was tested here. Further data are required to examine equitability between partners in more detail in a variety of species.

Chapter 4

General Discussion

In common with most seabirds, gannets exhibit bi-parental care, with both parents making a large contribution to chick-rearing. The traditional explanation for bi-parental care has been that a large input by both parents is required to successfully raise offspring to fledging. However, there are alternative hypotheses that have not been adequately addressed. For instance, synchronous ovulation by females may effectively eliminate the ability of males to participate in polygynous matings. Moreover, twinning experiments have demonstrated that parents can raise two offspring successfully (Northern Gannets, Nelson 1978; Cape Gannets *Morus capensis*, Navarro 1991), implying that one parent could raise a single chick.

In this study adults spent very little time together at the nest until chicks attained fledging age (*Chapter 3*). Average foraging trip durations were similar to those recorded in a number of previous studies (Table 6 in Nelson 1978b), and were less than half as long as those recorded by Hamer *et al.* (2000) at a colony with normal chick growth and fledging success. Thus, data for Great Saltee were probably collected under normal conditions of food supply, and suggest that gannets have very little leeway to increase their time spent foraging without leaving chicks unattended. This is consistent with the notion that both parents are required to provide sufficient food for the chick. This notion does not appear to be supported by twinning experiments (Nelson 1978; Navarro 1991). However, the latter took no account of the impact of artificial twinning on the future reproductive output of parents or post-fledging survival of chicks. In a similar experiment, Perrins *et al.*

(1973) found that Manx Shearwaters (*Puffinus puffinus*) were able to rear two chicks to fledging, but that twinned chicks had low body masses and poor post-fledging survival. This suggests that whilst parents might be capable of rearing two chicks, such chicks would contribute little to the parents' evolutionary fitness.

Older chicks were sometimes left unattended in this study (*Chapter 3*) and they were frequently attacked by non-breeders and neighbouring conspecifics. Thus in addition to food-provisioning requirements, bi-parental care in gannets, and possibly other species, may be related to the need to have one parent protecting the chick at all times, especially during early chick-rearing. This is supported by a study of Blue-eyed Shags (*Phalacrocorax atriceps*; Bernstein and Maxson 1984) which found that chicks were almost always attended by at least one parent, and those that were not attended were attacked by conspecifics. However the requirement to have one parent foraging and the other protecting the chick may not explain the preponderance of bi-parental care in burrow-nesting seabirds.

Male gannets made shorter foraging trips than females and thus delivered food to the nest more frequently. Females might be expected to spend more time foraging for themselves in order to regain body reserves used in egg production (Harris 1966; Hatch 1990), but given the long incubation periods of gannets and the small size of the egg as a proportion of female body size (*Chapter 1*), it is unlikely that egg production meant that females were in poorer condition than males by the start of chick-rearing. In other species males appear to forage more efficiently

than females (Weimerskirch *et al.* 1997; Gray and Hamer in press), but further data are required on meal sizes and changes in body mass during foraging trips, to determine whether or not this is the case in Gannets. Longer foraging trips by females may also have reduced competition with males for food resources close to the colony, as occurs in Giant Petrels (*Macronectes halli*; Hunter 1983), although this seems unlikely given the similarity in body sizes of males and females (*Chapter 2*).

Males at Great Saltee spent a greater proportion of their time at the nest site than females during chick-rearing, whereas a study by Montevecchi and Porter (1980) in Newfoundland found the opposite. This may indicate that the roles of males and females during chick-rearing can differ from one colony to another.

However, the data from Newfoundland were based on very short observation periods (1 – 16 hours) and indicated an average trip duration of only three hours, which is much shorter than the average recorded at other gannet colonies (Nelson 1978b; Wanless 1981; Hamer *et al.* 2000; this study). The data from Newfoundland should thus be viewed with some caution. Gilardi (1992) found from transect surveys that female Brown Boobies (*Sula leucogaster*) foraged further from the colony than males during the breeding season, which is consistent with the pattern recorded for gannets at Great Saltee.

Intraspecific variation in niche utilization in birds is presumed to be related mainly to differences in body size (Selander 1966; Ingolfsson 1969). Hence,

previous studies of chick-rearing behaviour of males and females have focused mainly on species with a high degree of sexual size dimorphism (Croxall and Prince 1980; Hunter 1984; Prince *et al.* 1992; Gonzalez-Solis 2000). Few studies have examined food delivery patterns of males and females in seabird species with negligible sexual size dimorphism. One such species is the Manx Shearwater. In this species, males spend more time incubating than females (Harris 1966), and return to the nest more frequently and deliver more food to the chick than females (Gray and Hamer in press). There is now a need for further data to examine the roles of male and female parents in other species with negligible sexual size dimorphism and to determine whether shorter foraging trips by males are a general pattern among seabirds.

A number of studies have examined the responses of seabird parents to experimentally induced changes in food requirement at the nest, and these studies have found conflicting results: in some cases, parents adjusted their rate of food delivery to compensate for changes in food requirement (Schreiber 1996; Hamer and Hill 1997; Weimerskirch *et al.* 1999). However, in other cases, parents either did not or could not respond to changes in food requirement at the nest (Hamer and Hill 1994; Weimerskirch *et al.* 2000). To my knowledge, no previous study has examined the responses of male and female parents separately, but the results of my study suggest that males and females might be expected to respond differently to experimental manipulation. This could be examined either by manipulating chicks at nests where both parents are marked and of known sex, or

by manipulating male and female parents separately (for instance by trimming primary feathers or attaching weights to birds; Wright and Cuthill 1989).

An increase in reproductive success with increasing age and experience has been reported in many seabird species (see reviews by Wooller *et al.* 1992; Hamer *et al.* in press). However, to my knowledge there are no data that describe changes with parental age in the contributions to chick-rearing by males and females.

While my study was able to quantify nest attendance patterns and foraging trip durations for known individuals during one breeding season, further work is necessary to determine how adult age and experience influence levels of co-operation between partners, and how the latter influences life-time reproductive success. The roles of males and females in chick-rearing have been insufficiently studied in seabirds, and further work in this field could make a large contribution to understanding the evolution of seabird life-histories and mating systems, and the interactions between seabirds and the marine environment.

References

- Ainley, D. G. and Schlatter, R. P. (1972) Chick raising ability in Adelie Penguins. *The Auk* **89**: 559-577.
- Alatalo, R. V., Burke, T., Dann, J., Hanotte, H., J., Lundberg, A., Moss, R. and Rintamaki, P. T. (1996) Paternity, copulation disturbance and female choice in lekking Black Grouse. *Animal Behaviour* **52**: 861-873.
- Anderson, D. J., Sievert, P. R., Andrews Labenski, J. and Ricklefs, R. E. (1991) A miniature activity recorder for plunge diving seabirds. *The Auk* **108**(2): 257-263.
- Arcese, P. (1989) Intrasexual competition and the mating system in primarily monogamous birds: the case of the Song Sparrow. *Animal Behaviour* **38**: 96-111.
- Baker, A. J., Piersma, T. and Greenslade, A. D. (1999) Molecular vs. phenotypic sexing in Red Knots. *The Condor* **101**: 887-893.
- Barrett, R. T., Peterz, M., Furness, R. W. and Durinck, J. (1989) The variability of biometric measurements. *Ringing and Migration* **10**: 13-16.
- Bernstein, N. P., Maxson, S. J. (1984) Sexually distinct daily activity patterns of Blue-eyed Shags in Antarctica. *The Condor* **86**: 151-156.
- Berrow, S. D., Humpidge, R. and Croxall, J. P. (2000) Influence of adult breeding experience on growth and provisioning of Wandering Albatross *Diomedea exulans* chicks at South Georgia. *Ibis* **142**: 199-207.

- Birkhead, T. R., Hatchwell, B. J., Lindner, R., Blomqvist, D., Pellatt, E. J., Griffiths, R., Lifjeld, J. T. (2001) Extra-pair paternity in the Common Murre. *The Condor* **103**: 158-162.
- Birt-Friesen, V. L., Montevecchi, D. K., Cairns, and Macko, S. A. (1989) Activity - specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* **70**(2) 357-367.
- Black, J. M., Ed. (1996) Introduction: Pair bonds and partnerships. In: *Partnerships in Birds: The Study of Monogamy*. Oxford Ornithology Series, Oxford, Oxford University Press. pp. 3-20.
- Black, J. M., Choudhury, S., Owen, M. (1996) Do Barnacle Geese benefit from lifelong monogamy? In *Partnerships in Birds: The Study of Monogamy*. (ed. J. M. Black) Oxford, Oxford University Press. pp. 91-117.
- Blondel, J., Perret, P., Galan, M. J. (2000) High divorce rates in Corsican Blue Tits: how to choose a better option in a harsh environment. *Oikos* **89**: 451-460.
- Boersma, P. D. and Davies, E. M. (1987) Sexing monomorphic birds by vent measurements. *The Auk* **104**: 779-783.
- Bolton, M. (1995) Food delivery to nestling Storm Petrels: Limitation or regulation? *Functional Ecology* **9**: 161-170
- Brown, K. (1998) Proximate and ultimate causes of adoption in Ring-billed Gulls. *Animal Behaviour* **56**: 1529-1543.

- Bukacinski, D., Bukacinska, M., Lugjuhn, T. (2000) Adoption of chicks and the level of relatedness in Common Gull, *Larus canus*, colonies: DNA fingerprinting analyses. *Animal Behaviour* **59**: 289-299
- Burger, J. (1986) Selection for equitability in some aspects of reproductive investment in Herring Gulls *Larus argentatus*. *Ornis Scandinavica* **18**: 17-23.
- Catry P., Ratcliffe, N., Furness, R. W. (1997) Partnerships and mechanisms of divorce in the Great Skua. *Animal Behaviour* **54**: 1474-1487.
- Charlesworth, B. and Leon, J. A. (1976) The relation of reproductive effort to age. *The American Naturalist* **110**(973): 449-459.
- Charnov, E. L. and Krebs, J. R. (1974) On clutch-size and fitness. *Ibis* **116**: 217-219.
- Chase, I. D. (1980) Cooperative and non-cooperative behavior in animals. *The American Naturalist* **115**(6): 827-857.
- Coulson, J. C. (1966) The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *Journal of Animal Ecology* **35**: 269-279
- Coulson, J. C. and Porter, J. M. (1985) Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* **127**: 450-466.
- Cramp, S. (1985) *The Birds of the Western Palaearctic*. Oxford, Oxford University Press.

- Croxall, J. P. and Prince, P. A. (1980) Food, feeding ecology and ecological segregation of seabirds of the Southern Hemisphere. *Oikos* **68**: 139-145.
- Croxall, J. P. and Ricketts, C. (1983) Energy costs of incubation in the Wandering Albatross *Diomedea exulans*. *Ibis* **125**: 33-39.
- Croxall, J. P., Rothery, P. and Crisp, A. (1992) The effect of maternal age and experience on egg-size and hatching success in Wandering Albatrosses *Diomedea exulans*. *Ibis* **134**: 219-228.
- Croxall, J. P., Hall, A. J., Hill, H. J., North, A. W., and Rodhouse, P. G. (1995) The food and feeding ecology of the White-chinned Petrel *Procellaria aequinoctialis* at South Georgia. *Journal of Zoology* **237**: 133-150.
- Curio, E. (1983) Why do young birds reproduce less well? *Ibis* **125**: 400-403.
- Drent, R. H. and Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225-252.
- Ellegren, H. and Sheldon, B. C. (1997) New tools for sex identification and the study of sex allocation in birds. *Trends in Ecology and Evolution* **12**: 255-259.
- Emlen, S. T. and Oring, L. W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* **197**(4300): 215-223.
- Erikstad, K. J., Fauchald, P., Tveraa, T., Steen, H. (1998) On the cost of reproduction in long-lived birds: The influence of environmental variability. *Ecology* **79**(5): 1781-1788.

- Furness, R. W. and Monaghan, P. (1987) *Seabird Ecology*. Glasgow, Blackie and Son Ltd.
- Garthe, S., Benvenuti, S., and Montevecchi, W. A. (2000) Pursuit plunging by Northern Gannets (*Sula bassana*) feeding on Capelin (*Mallotus villosus*). *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**(1454): 1717-1722.
- Gaston, A. J., Eberl, M., Hipfner and Lefevre, K. (1995) Adoption of chicks among Thick-billed Murres. *The Auk* **112**: 508-510.
- Gilardi, J. D. (1992) Sex-specific foraging distributions of Brown Boobies in the Eastern Tropical Pacific. *Colonial Waterbirds* **15**(1):148-152.
- Gonzalez-Solis, J., Croxall, J. P. and Wood, A. G. (2000) Sexual dimorphism and sexual segregation in foraging strategies of Northern Giant Petrels, *Macronectes halli*, during incubation. *Oikos* **90**: 390-398.
- Goodman, D. (1974) Natural selection and a cost ceiling on reproductive effort. *The American Naturalist* **108**(961): 247-269.
- Gowaty, P. A. (1996) Battles of the sexes and origins of monogamy. In: *Partnerships in birds: the study of monogamy*. (ed. J. M. Black). Oxford, Oxford University Press. pp. 21-52.
- Granadeiro J. P., Bolton M., Silva M. C., Nunes M., Furness R. W. (2000) Responses of breeding Cory's Shearwater *Calonectris diomedea* to experimental manipulation of chick condition. *Behavioural Ecology*, **11**(3): 274-281.

- Grant, B. R. and Grant, P. R. (1987) Mate choice in Darwin's finches. *Biological Journal of the Linnean Society* **32**: 27-270.
- Gray, C. M. and Hamer, K. C. (in press) Food provisioning behaviour of male and female Manx Shearwaters *Puffinus puffinus*. *Animal Behaviour*.
- Griffiths, R. and Tiwari, B. (1995) Sex of the last wild Spix's Macaw. *Nature* **375**(454).
- Griffiths, R., Tiwari, B. and Becher, S. A. (1992) The identification of sex in the Starling *Sturnus vulgaris* using a molecular DNA technique. *Molecular Ecology* **1**: 191-194.
- Griffiths, R., Double, M. C., Orr, K. and Dawson, R. J. G. (1998) A DNA test to sex most birds. *Molecular Ecology* **7**: 1071-1075.
- Hamer, K. C. and Furness, R. W. (1991) Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *Journal of Animal Ecology* **60**: 693-704.
- Hamer, K. C. and Hill, J. K. (1994) The regulation of food delivery to nestling Cory's Shearwaters *Calonectris diomedea*: the roles of parents and offspring. *Journal of Avian Biology* **25**: 198-204.
- Hamer, K. C. and Hill, J. K. (1997) Nestling obesity and variability of food delivery in Manx Shearwaters, *Puffinus puffinus*. *Functional Ecology* **11**: 489-497.
- Hamer K. C.; Thompson D. R. (1997) Provisioning and growth rates of nestling Fulmars *Fulmarus glacialis*: Stochastic variation or regulation? *Ibis* **139**(1): 31-39.

- Hamer, K. C., Nicholson, L. W., Hill, J. K., Wooller, R. D., and Bradley, J. S. (1997) Nestling obesity in procellariiform seabirds: temporal and stochastic variation in provisioning and growth of Short-tailed Shearwaters *Puffinus tenuirostris*. *Oecologia* **112**: 4-11.
- Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P. and Wood, A. G. (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series* **200**: 257-264.
- Hamer, K. C., Schreiber, B. A., Burger, J. (in press) Breeding biology, life histories and life history-environmental interactions in seabirds. In *Biology of Marine Birds* (eds. B. A. Schreiber, J. Burger), Florida, U.S.A. CRC Press
- Harris, M. P. (1966) Breeding biology of Manx Shearwaters (*Puffinus puffinus*). *Ibis* **108**: 17-33.
- Hatch, S. A. (1990) Incubation rhythm in the Fulmar *Fulmarus glacialis*: annual variation and sex roles. *Ibis* **132**: 515-524.
- Hedd, A., Gales, R. P. and Brothers, N. P. (1998) Reliability of morphometric measures for determining the sex of adult and fledgling Shy Albatrosses, *Diomedea cauta cauta*, in Australia. *Wildlife Research* **25**: 69-79.
- Houston, A. I. and Davies, N. B. (1985) The evolution of cooperation and life history in the Dunnock *Prunella modularis*. In *Behavioural Ecology: Ecological consequences of adaptive behaviour*. (eds. R. M. Sibly and R. H. Smith). Oxford, Blackwell Scientific Publications. pp. 471-487.

- Hunter, S. (1983) The food and feeding ecology of the Giant Petrels *Macronectes halli* and *M. giganteus* at South Georgia. *Journal of Zoology* **200**: 521-538.
- Hunter, S. (1984) Breeding biology and population dynamics of Giant Petrels *Macronectes* at South Georgia (Aves: Procellariiformes). *Journal of Zoology* **203**: 441-460.
- Ingolfsson (1969) Sexual dimorphism in Gulls. *The Auk* **86**: 732-737.
- Jodice, P. G. R., Lanctot, R. B., Gill, V. A., Roby, D. D., Hatch, S. A. (2000) Sexing adult Black-legged Kittiwakes by DNA, behavior and morphology. *Waterbirds* **23**(3): 405-415.
- Jones, D. and Birks, S. (1992) Megapodes-Recent ideas on origins, adaptations and reproduction. *Trends in Ecology and Evolution* **7**(3): 88-91.
- Jonsson, L. (1993) *Birds of Europe (with North Africa and the Middle East)*. London, Christopher Helm.
- Jouventin, P., Lequette, B. and Dobson, S. (1999) Age-related mate choice in the Wandering Albatross. *Animal Behaviour* **57**(5): 1099-1106.
- Klecka, W. R. (1980) *Discriminant Analysis*. Beverly Hills, USA, Sage Publications Inc.
- Lack, D. (1968) *Ecological adaptations for breeding in birds*. London, Methuen & Co. Ltd.
- Lessells, C. M. and Mateman, A. C. (1998) Sexing birds using random amplified polymorphic DNA (RAPD) markers. *Molecular Ecology* **7**: 187-195.

- Linden M. (1991) Divorce in Great Tits - chance or choice? An experimental approach. *American Naturalist* **138**: 147-163.
- Martin, T. E. (1987) Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecological Systems* **18**: 453-487.
- Martin, K. (1995) Patterns and mechanisms for age-dependent reproduction and survival in birds. *American Zoologist* **35**: 340-348.
- Millar, C. D., Lambert, D. M., Anderson, S. and Halverson, J. L. (1996) Molecular sexing of the communally breeding Pukeko: An important ecological tool. *Molecular Ecology* **5**(2): 289-293.
- Mills, J.A., Yarrell, J.W., Mills, D.A. (1996) Causes and consequences of mate fidelity in Red-billed Gulls. In: *Partnerships in birds: the study of monogamy*. (ed. J. M. Black). Oxford, Oxford University Press. pp. 286-304.
- Mock, D. and Fujioka, M. (1990) Monogamy and long term pair bonding in vertebrates. *Trends in Ecology and Evolution* **5**: 39-43.
- Mock, D. and Ploger, B. J. (1987) Parental manipulation of optimal hatch asynchrony in Cattle Egrets: an experimental study. *Animal Behaviour* **35**: 150-160.
- Mock, D. W., Schwagmeyer, P. L. and Parker, G. A. (1996) The model family. In: *Partnerships in Birds: The Study of Monogamy*. (ed. J. M. Black). Oxford, Oxford University Press.
- Montevecchi, W. A. and Porter, J. M. (1980) Parental investments by seabirds at the breeding area with emphasis on Northern Gannets, *Morus bassanus*. In

- Behaviour of Marine Animals, Current Perspectives in Research. 4 Marine Birds.* (eds. J. Burger, B. L. Olla and H. E. Winn). London, Plenum Press. pp. 323-365.
- Navarro, R. A. (1991) Food addition and twinning experiments in the Cape Gannet: Effects on breeding success and chick growth and behavior. *Colonial Waterbirds* **14**(2): 92-102.
- Nelson, J. B. (1964) Factors influencing clutch-size and chick growth in the North Atlantic Gannet *Sula bassana*. *Ibis* **106**: 63-77.
- Nelson, J. B. (1965) The behaviour of the gannet. *British Birds* **58**(7): 233-287.
- Nelson, J. B. (1978) *The Sulidae: Gannets and Boobies*. Oxford, Oxford University Press.
- Nelson, J. B. (1978b) *The Gannet*. Berkhamsted, U.K., T&AD Poyser Ltd.
- Nisbet, I. C. T., Hatch, J. J. (1999) Consequences of female-biased sex-ratio in a socially monogamous bird: female-female pairs in the Roseate Tern (*Sterna dougallii*). *Ibis* **141**: 307-320.
- Norusis, M. J. (2000) *SPSS 10.0 Guide to Data Analysis*. London, Prentice Hall.
- Orians, G. H. (1969) On the evolution of mating systems in birds and mammals. *American Naturalist* **103**: 589-603.
- Orians, G. H. and Pearson, N. E. (1979) On the theory of central place foraging. *Analysis of Ecological Systems*. (ed. D. J. Horn, R. D. Mitchell and G. R. Stairs). Columbus, Ohio State University Press. pp. 155-177.

- Parker, G. A. (1979) Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects* (ed. M. S. Blum and N. A. Blum), New York, Academic Press. pp. 123-66.
- Parker, G. A. and Mock, D. W. (1987) Parent-offspring conflict over clutch size. *Evolutionary Ecology* **1**: 161-174.
- Perrins, C. M., Harris, M. P., Britton, C. K. (1973) Survival in Manx Shearwaters. *Puffinus puffinus*. *Ibis* **115**: 535-548.
- Phillips, R. A. and Furness, R. W. (1998) Repeatability of breeding parameters in Arctic Skuas. *Journal of Avian Biology* **29**: 190-196.
- Phillips, R. A., Hamer, K. C. (2000) Growth and provisioning strategies of Northern Fulmars *Fulmarus glacialis*. *Ibis* **142**: 435-445.
- Prince, P. A., Wood, A. G., Barton, T. R. and Croxall, J. P. (1992) Satellite-tracking Wandering Albatrosses *Diomedea exulans* in the South Atlantic. *Antarctic Science* **4**: 31-36.
- Ricklefs, R. E. (1977) Composition of eggs of several bird species. *The Auk* **94**: 350-356.
- Ricklefs, R. E. (1979) Adaptation, constraint, and compromise in avian postnatal development. *Biology Review* **54**: 269-290.
- Ricklefs, R. E. and Montevecchi, W. A. (1979) Size, organic composition and energy content of North Atlantic Gannet *Morus bassanus* eggs. *Comparative Biochemistry and Physiology* **64A**: 161-165.

- Ryder, J. P. and Somppi, P. L. (1979) Female-female pairing in Ring-billed gulls. *Auk* **96**: 1-5.
- Saino, N., Fasola, M., Crocicchia, E. (1994) Adoption behaviour in Little and Common Terns (Aves, *Sternidae*) - Chick benefits and parents fitness costs. *Ethology* **97**(4): 294-309.
- Siegel, S. (1956) *Nonparametric Statistics for the Behavioral Sciences*. New York, McGraw-Hill.
- Selander, R. K. (1966) Sexual dimorphism and differential niche utilization in birds. *The Condor* **68**(2): 113-151.
- Schreiber, E. A. (1996) Experimental manipulation of feeding in Red-tailed Tropicbird chicks. *Colonial Waterbirds* **19**(1): 45-55.
- Sokal, R.R., Rohlf, F.J. (1981) *Biometry*. New York, Freeman and Co.
- Starck, J. M. and Ricklefs, R. E. (1998) *Avian Growth and Development*. Oxford, Oxford University Press.
- Sydeman, W. J., Pyle, P., Emslie, S. D., McLaren, E. B. (1996) Causes and consequences of long-term partnerships in Cassin's Auklets. In *Partnerships in Birds: The Study of Monogamy*. Oxford, (ed. J. M. Black) Oxford University Press. pp. 211-222
- Thompson, K. R., Brindley, E. and Heubeck, M. (1998) *Seabird numbers and breeding success in Britain and Ireland, 1997*. Peterborough, Joint Nature Conservation Committee. (UK Nature Conservation, No. 22.)

- Trivers, R. L. (1972) Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*. (ed. B. G. Campbell). Chicago, Aldine Press. pp. 136-179.
- Veiga, J. P. (1992) Why are house sparrows predominantly monogamous? A test of hypotheses. *Animal Behaviour* **43**: 361-370.
- Wanless, S. (1981) The gannets of Boreray. In: *The Boreray 1980 expedition. A report on the ecology and natural history of St. Kilda University of Durham, Durham. (unpublished expedition report)*. pp. 26-28.
- Weimerskirch, H. (1992) Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* **64**(3): 464-473.
- Weimerskirch (1995) Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* **102**: 37-43.
- Weimerskirch, H. (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. *Journal of Animal Ecology* **67**: 99-109.
- Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenot-Chaillet, F., Hindermeyer, X. and Judas, J. (1994) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* **47**: 472-476.
- Weimerskirch, H., Cherel, Y., Cuenot-Chaillet, F., Ridoux, V. (1997) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* **78**(7): 2051-2063.

- Weimerskirch, H., Fradet, G. and Cherel, Y. (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic Prion. *Journal of Avian Biology* **30**: 165-174.
- Weimerskirch, H., Prince, P. A. and Zimmermann, L. (2000) Chick provisioning by the Yellow-nosed Albatross *Diomedea chlorohychnos*: response of foraging effort to experimentally increased costs and demands. *Ibis* **142**: 103-110.
- Wendeln, H. and Becker, P. H. (1999) Effects of parental quality and effort on the reproduction of Common Terns. *Journal of Animal Ecology* **68**: 205-2114
- Wolf, J.B., Brodie, E.D. III., Cheverud, J.M., Moore, A.J., Wade, M.J. (1998) Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution*. **13**: 64-69.
- Wooller, R. D. and Bradley, J. S. (1996) Monogamy in a long-lived seabird: the Short-tailed Shearwater. In *Partnerships in birds: the study of monogamy*. (ed. J. M. Black). Oxford, Oxford University Press. pp. 223-235.
- Wooller, R. D., Bradley, J. S., Croxall, J. P. (1992) Long-term population studies of seabirds. *Trends in Ecology and Evolution* **7** (4): 111-114.
- Wright, J. and Cuthill, I. (1989) Manipulation of sex differences in parental care. *Behavioural Ecology and Sociobiology* **25**: 171-181.
- Young, E. C. (1978) Behaviour of *lonnbergi* skuas in relation to environment on the Catham Islands, New Zealand. *New Zealand Journal of Zoology* **5**: 401-416.
- Zar, J. H. (1996) *Biostatistical Analysis*. Prentice Hall International Inc., London.

